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The Demography and Determinants of Population Growth in Utah Moose (*Alces Alces Shirasi*)

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THE DEMOGRAPHY AND DETERMINANTS OF POPULATION GROWTH IN UTAH MOOSE (*ALCES ALCES SHIRASI)*

by

Joel S. Ruprecht

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ABSTRACT

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in Utah Moose (*Alces alces shirasi*)

by

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Utah State University, 2016

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Moose in Utah represent the southernmost naturally occurring populations of moose in the world. Concerns over possible numeric declines and a paucity of baseline data on moose in the state prompted the Utah Division of Wildlife Resources to initiate a study of moose demography in collaboration with Utah State University. The objectives of this study were to 1) determine reproductive rates of moose in Utah and the factors which influence them, and 2) combine aerial count data from multiple management units within the state to identify factors which influence interannual variation in population growth rates.

We constructed generalized linear models to relate maternal body condition and age to reproductive success. We found that body condition ($P = 0.01$) and age ($P = 0.02$) contributed significantly to the probability of pregnancy and the best model describing this relationship was nonlinear. Body condition also related positively to subsequent

calving ($P = 0.08$) and recruitment ($P = 0.05$), but model selection suggested the relationship for these metrics was best described by linear models. A meta-analysis of moose reproductive rates in North America suggested that reproductive rates declined significantly with latitude ($P \leq 0.01$), i.e. as populations approached their southern range limit.

We used Bayesian state-space models to combine moose count data from different management units to estimate statewide population dynamics between 1958 and 2013. This approach incorporated uncertainty in population counts arising from observation error. Population density and warm winter temperatures negatively influenced population growth rate with a high degree of confidence; 95% Bayesian Credible Intervals for these variables did not overlap zero. Short-term projections of moose abundance in the state suggested that the population will likely remain stable despite projected increases in winter temperature.

Results from this study will aid managers in achieving management objectives as well as future decision making. The unique characteristics of the population also have application toward understanding the dynamics of populations of cold-adapted species at their southern range limit.

(129 pages)

PUBLIC ABSTRACT

The Demography and Determinants of Population Growth

in Utah Moose (*Alces alces shirasi*)

Joel S. Ruprecht

Moose (*Alces alces*) occur widely in northern regions of the world. Across their distribution, the species is considered to be of high intrinsic, ecological and recreational value. Populations of moose along their southern range limit in North America have shown erratic population dynamics in recent decades including severe numeric declines in some areas. Moose in Utah belong to the Shiras subspecies, which is a relatively understudied population segment. Additionally, moose in Utah represent the southernmost naturally occurring moose populations worldwide. Concerns over possible declines and a paucity of baseline data on moose within the state prompted the Utah Division of Wildlife Resources to initiate a demographic study of moose in collaboration with Utah State University.

We estimated vital rates including pregnancy, calving, recruitment and adult female survival. Consistent with the theory on life history strategies of large herbivores, we found high adult survival rates but variable reproductive rates. Maternal age and body condition influenced reproductive success. A meta-analysis indicated that southern moose populations in North America tended to be lower than those in more northerly areas.

Using a long-term dataset of aerial moose counts in Utah, we determined factors that influenced interannual variation in population growth rates. Population density,

warm winter temperatures, and human harvest all negatively affected population growth rate. However, projections of future moose abundance in the state suggest that the population will likely remain stable in the short-term future if harvest rates are conservative.

Results from this study will aid managers in achieving management objectives as well as future decision making. The unique characteristics of the population also have application toward understanding the dynamics of populations of cold-adapted species at their southern range limit.

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Joel Ruprecht

CONTENTS

Page

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

INTRODUCTION

Moose (*Alces alces*) are the largest species of the deer family (Cervidae) and occupy a circumpolar distribution spanning the continents of North America, Europe, and Asia (Telfer 1984). Moose first colonized North America an estimated 11,000–14,000 years ago by crossing the Bering Strait from Eurasia into present day Alaska (Hundertmark et al. 2002). From there, moose expanded southward during inter-glacial periods, and presently occupy the majority of Alaska and Canada, as well as the northern fringes of the lower 48 states (Kelsall and Telfer 1974). Moose are supremely adapted to living in cold and wet environments; as such, their distribution largely coincides with the occurrence of boreal forest and is thought to be limited by warm and arid conditions to the south (Kelsall and Telfer 1974; Telfer 1984).

Four subspecies are currently recognized in North America: Alaskan moose (*Alces alces gigas*), the northwestern moose (*Alces alces andersoni*), the eastern moose (*Alces alces americana*), and the Shiras moose (*Alces alces shirasi*; Bubenik 2007). The southernmost subspecies, Shiras moose, occupy the Rocky Mountains of southwestern Canada and the northwestern United States. This subspecies naturally colonized states in the intermountain west (Wyoming and Utah) only within the last century and a half (Brimeyer and Thomas 2004; Wolfe et al. 2010), and was more recently introduced into Colorado (Olterman et al. 1994). Moose in Utah represent the southernmost naturally-occurring moose population in the world (Wolfe et al. 2010).

On a broad scale, moose populations in North America are thought to be stable (Peek et al. 1998). However, drastic declines in certain areas have been noted. In particular, Minnesota has experienced alarming declines in moose numbers in recent decades (Murray et al. 2006; Lenarz et al. 2010; DelGiudice et al. 2011). In addition, more moderate declines have been noted in Montana (DeCesare et al. 2014), Wyoming (Brimeyer and Thomas 2004) and parts of Canada (Patterson et al. 2013).

Factors limiting moose populations have been assessed in studies elsewhere. Density-dependent resource limitation is thought to occur widely and is mediated through both changes in population density and environmental stochasticity (Sæther 1997; Solberg et al. 1999; Vucetich and Peterson 2004; Brown 2011). Parasites and disease have both caused declines in moose populations (Murray et al. 2006; Lankester 2010) but is highly variable according to the geographic occurrence of the disease or parasite. In predator-abundant areas, predation is thought to limit moose populations (Bergerud et al. 1983; Gasaway et al. 1992; Bertram and Vivion 2002), although whether this mechanism is limiting or regulating is debated (Bergerud and Snider 1988; Thompson and Peterson 1988; Van Ballenberghe and Ballard 1994). Similarly, human harvest can limit population growth (Solberg et al. 1999), although harvest serves as an effective management tool to increase per-capita resource availability (Boertje et al. 2007). Finally, abiotic factors such as climate are thought to limit moose at range peripheries (Kelsall and Telfer 1974; Murray et al. 2006).

As with other large herbivores, adult female survival rates in moose are typically constant and robust to changes in environmental conditions (Gaillard et al. 2000;

Bonenfant et al. 2009). This is thought to be an evolved trait common to long-lived mammals which have low fecundity rates (Eberhardt 2002). As a result, under resource limitation, reproductive rates in moose are often reduced in favor of maintaining adult survival rates (Lenarz et al. 2010). Therefore, population growth rates are most sensitive to changes in adult female survival (Lenarz et al. 2010). However, because adult survival rates typically remain constant, much of the interannual variation in population growth rates are determined by reproductive output and juvenile survival (Gaillard et al. 2000; Raithel et al. 2007).

Managing harvested populations is most effective when based on principles of population biology (Mills 2012). In order to set and meet appropriate management objectives, wildlife managers require detailed information on the vital rates of populations within their jurisdiction (Mills 2012). However, the factors affecting vital rates can vary between different populations of the same species (Grøtan et al. 2009). As such, detailed studies are required at the level of the management jurisdiction.

In Utah, moose are considered to be of high intrinsic, ecological, and recreational value. Since 1958, the Utah Division of Wildlife Resources (UDWR) has permitted harvests of moose which have been administered as a “once in a lifetime” opportunity. Currently, the UDWR manages moose by maintaining a mean adult male (i.e. bull) age structure between 4-5 years old. The bull age structure is estimated by aging harvested moose annually. The UDWR then adjusts harvest permits accordingly to maintain the population within the target age structure. Female (i.e. cow) permits have been offered in the past, but since 2010 have been eliminated due to concerns regarding population

declines. The UDWR monitors trends in abundance through aerial counts of the management units where moose occur. These surveys are conducted on rotations in which each management unit is surveyed on average every 3 years.

Few formal studies have previously been conducted on moose in Utah. In the 1970s, two notable studies quantified the nutritional quality and biomass of browse species in the North Slope Unit which allowed estimation of ecological carrying capacity of moose (Wilson 1971; Babcock 1977). Babcock et al. (1982) subsequently evaluated harvest strategies for moose in Utah. These authors found some evidence that experimental reductions in the bull:cow ratio negatively affected recruitment rates. Wolfe et al. (2010) reviewed the history and management of moose in the state and evaluated potential limiting factors. However, detailed information on vital rates and population dynamics of moose in Utah were lacking, making a demographic study of moose within the state highly warranted. Therefore, in 2013 the UDWR initiated a study in collaboration with Utah State University, which is the subject of this thesis.

PURPOSE

This study seeks to fulfill two main research objectives utilizing data from both an ongoing telemetry study and historic count data. The first objective is to estimate current vital rates for moose in the North Slope of the Uintas and Wasatch Mountains Units. To accomplish this, the DWR deployed radiocollars on 60 female moose in each unit in 2013. The vital rates of interest include adult female survival, pregnancy, calving, and recruitment rates. Data on body condition and ages were also collected on a subset of

moose. Chapter 2 of this thesis examines relationships between age, body condition, and reproductive rates of radiocollared moose. However, because survival analyses of long-lived organisms require many years of data collection to make proper inference (Murray 2006), survival rates are not analyzed at this phase of the study. Nonetheless, annual survival estimates have been estimated between 2013 and 2015 and are presented in Appendix A (Table A.1).

The second objective of the study was to determine the factors affecting population growth rates, in which we utilized long-term data on moose counts in the state acquired by the DWR from aerial censuses. We combined count data across management units and used a modeling approach to incorporate imprecision in the counts. We assessed the influence of harvest, climate, and population density of the long-term growth rates of moose statewide. Then, using the best model describing observed rates of population growth, we made short-term projections of moose abundance. This analysis is the focus of Chapter 3.

Although this research is important primarily due to its relevance to management, the uniqueness of the population allows application to broader ecological themes. In particular, the characteristics of this study system provide a unique opportunity to study how a cold-adapted species performs at its southern range limit where environmental factors may be limiting. Thus, a common theme throughout this thesis is how the population dynamics of moose in Utah compare to those in the core of their range. Whether or not peripheral populations perform differently than those in the core of their range is a theme with deep roots in the field of ecology (Caughley et al. 1988) and is still

debated today (Talley 2007; Sexton et al. 2009). We seek to present results from this study in the context of this overarching theme.

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CHAPTER 2

REPRODUCTION IN MOOSE AT THEIR SOUTHERN RANGE LIMIT

ABSTRACT

Reproduction is a critical fitness component in large herbivores. Biogeographic models predict that range-edge populations may have compromised reproductive rates because of inferior habitat at range peripheries. When reproductive rates are chronically low, ungulate populations may lack the resiliency to rebound quickly after periods of environmental stress, and this effect may be greatest for heat-sensitive organisms at their southern range limit. To assess the demographic vulnerability of moose (*Alces alces*), we studied relationships between reproductive rates, maternal age, and rump fat in the southernmost naturally-occurring moose population in North America. For prime-aged moose in our study, pregnancy rates were high (92%), but moose aged < 3 or > 9 years had low pregnancy rates (32% and 38%, respectively). The relationship between rump fat and pregnancy was nonlinear such that a threshold of at least 2 mm of rump fat yielded a high probability of being pregnant midwinter. In contrast, among pregnant moose, the probability of both producing a calf and recruiting it until spring increased linearly with rump fat. We also conducted a meta-analysis of pregnancy and twinning rates for adult (≥ 2 years) moose across a latitudinal gradient to compare reproductive rates from our study to other populations in North American. Moose living at southern latitudes tended to have lower reproductive rates than those living in the core of moose range, implying that

southern moose populations may be demographically more vulnerable than northern moose populations.

INTRODUCTION

Understanding vulnerability of wildlife populations to environmental change is an urgent and worldwide conservation concern (Dawson et al. 2011). Biogeographic models predict that populations inhabiting the edge of a species range are demographically more vulnerable to environmental change than are populations at the range core because of inferior habitat conditions at the edge (Caughley et al. 1988; Lawton 1993; Channell and Lomolino 2000; Sagarin and Gaines 2002; Vucetich and Waite 2003). Reports of depressed reproduction in edge populations of some plants (Garcia et al. 2000; Jump and Woodward 2003; Angert 2006) and animals (Caughley et al. 1988; Sanz 1997) support this prediction. Little is known, however, about whether this biogeographic pattern applies to cold-adapted ungulate species, especially those with populations inhabiting low-latitude edges of the geographic range of the species. Low reproduction in these edge populations may limit the extent to which they can adapt to persistent climate warming and may presage a poleward range contraction (Hampe and Petit 2005).

Moose are a cold-adapted ungulate (Renecker and Hudson 1986) with a circumpolar distribution that reaches its lowest latitude in the southern Rocky Mountains of the United States (Telfer 1984). Range loss linked to low reproduction has been reported in moose inhabiting other portions of their southern range limit in North America, which includes southern Canada and the northcentral and northeastern

contiguous United States (Murray et al. 2006; Lenarz et al. 2010). Conversely, some southerly moose populations in western Canada and the northeastern United States have exhibited range expansion (Foster et al. 2002; Darimont et al. 2005; Musante et al. 2010) which suggests that reproductive success is independent of latitude and that the vulnerability of a population to environmental change is not easily generalized as a function of proximity to the range edge. Notably, little is known about the reproduction of Shiras moose (*Alces alces shirasi*), which is the Rocky Mountain subspecies that inhabits the southernmost reaches of the circumpolar distribution of the species.

Early studies of Shiras moose presented anecdotal evidence that reproductive rates were lower in southern-edge moose populations than those in the core of moose range (Peek 1962; Houston 1968; Peek 1974). It was thought that comparatively low reproductive output was either controlled by a genetic influence (Houston 1968) or arose from marginal habitat quality (Peek 1974). Despite the suggestion that moose reproductive rates may vary along a north-south gradient throughout North America, the hypothesis has never been tested. An important consequence of this knowledge gap means that if low reproductive rates are documented in southern moose populations, it is unclear whether the occurrence is an anomaly or instead a pervasive characteristic of southern moose populations.

Shiras moose have experienced declines in recruitment of young in many herds in Utah, Wyoming and Colorado in recent decades (Monteith et al. 2015). Monteith et al. (2015) observed lower recruitment after years that were warm, dry, or exhibited rapid rates of spring greenup. Such climatic conditions likely reduced forage quantity and

quality which acted to suppress maternal nutritional condition, ultimately at the expense of recruiting young (Monteith et al. 2015). Future climatic conditions in this region are expected to become warmer (Gutzler and Robbins 2011) and drier (Cook et al. 2015), which could continue to exacerbate nutritional intake for moose. Therefore, understanding the extent to which various reproductive rates are influenced by maternal body condition will help elucidate how productivity of moose populations may change in response to a declining nutritional plane.

Here, we seek to fulfill two objectives related to moose reproduction. First, we clarify the extent to which pregnancy, parturition, and recruitment rates are influenced by nutritional condition in Shiras moose. Rump fat is a strong predictor of nutritional condition (Stephenson et al. 1998) and subsequent reproductive success in Alaskan moose (*Alces alces gigas*; Testa and Adams 1998; Keech et al. 2000) but this pattern has not been described in Shiras moose, or more generally, moose at their southern range limit. Second, we tested the hypothesis that reproductive rates are lower for moose populations near the southern range limit by assessing whether there is a latitudinal trend in fecundity rates using data obtained from a meta-analysis. Results from this study will contribute to a better understanding of the resiliency of this cold-adapted species at its southern range limit to future environmental stress.

METHODS

Study area.—We studied moose in two mountain ranges in northern Utah: the Wasatch Mountains (40.4° N, -111.3° W) and the North Slope of the Uinta Mountains

(40.9° N, -110.5° W). Study areas were bounded by the North Slope and Wasatch Mountains management units and together comprise > 5,000 km^2. Moose in our study represented the southernmost naturally-occurring moose populations in North America. Although moose currently occupy more southerly latitudes in Colorado, those herds were introduced into the state by means of transplants from Utah (Olterman et al. 1994).

The North Slope Unit was characterized by high elevation (2,500–3,500 m) montane forest with much of the suitable habitat contained within the High Uintas Wilderness. The forested areas were dominated by lodgepole pine (*Pinus contorta*) interspersed with quaking aspen (*Populus tremuloides*), and subalpine fir (*Abies lasiocarpa*) occurred at higher elevations. Forested areas were punctuated by several wide drainages that created expansive riparian willow (*Salix* spp.) communities. Lakes and marshes were common in the high elevation areas. In contrast, the Wasatch Unit was composed of a more heterogeneous landscape, and included mid- to high-elevation (2,000–3,000 m) zones, much of which was atypical moose habitat. Lower elevation areas were characterized by sagebrush steppe (*Artemesia* spp.) communities with Gambel oak (*Quercus gambelii*) and mountain mahogany (*Cercocarpus* spp.) occurring in high abundance, and transitioned into higher elevation habitat composed of Douglas fir (*Pseudotsuga menziesii*), lodgepole pine, and aspen. Willow communities were present, but occurred in low densities throughout the Wasatch Mountains. In the eastern portion of the unit, juniper (*Juniperus* spp.) and pinyon pines (*Pinus edulis*) were common.

Data obtained from the National Oceanic and Atmospheric Administration/National Climatic Data Center (NOAA/NCDC) nClimDiv dataset (Vose

et al. 2014) indicated historic seasonal temperatures for the study area (Utah Northern Mountains climate division) averaged 8.1°, 15.1°, –0.4°, and –5.2°C for spring, summer, fall, and winter, respectively. Historic total seasonal precipitation averaged 15.1, 10.8, 16.7, and 11.3 cm during the same seasons. Climatic conditions in the year before our study were generally warmer and drier than the historic means: temperatures averaged 9.9°, 16.5°, 0.8°, and –6.8°C for spring, summer, and fall 2012, and winter 2013, respectively, while total seasonal precipitation was 6.4, 9.3, 16.9, and 6.0 cm during the same seasons.

The North Slope was the first area in Utah to be colonized by moose, which occurred through natural dispersal from the Greater Yellowstone Ecosystem in the early 1900s (Wolfe et al. 2010). Subsequently, moose dispersed to other areas of the state including the Wasatch Mountains, and some herds were augmented by management translocations conducted by the Utah Division of Wildlife Resources. Although moose were introduced to parts of the state farther south than our study area, none of those herds have established viable populations; thus, the likely range limit for moose in Utah occurs at about 40°N (Wolfe et al. 2010).

Capture and handling.—We captured 120 female moose in January and February 2013 as part of a multi-year study of moose demography in Utah. Each moose was fit with a very-high-frequency (VHF) radiocollar with mortality-motion sensors (Sirtrack Ltd., Havelock North, New Zealand). We determined the pregnancy status of all captured moose using the pregnancy-specific protein B (PSPB) assay on serum obtained from blood samples collected from venipuncture (BioTracking, Moscow, Idaho, USA–Sasser

et al. 1986; Haigh et al. 1993). Of these 120 moose, we extracted the incisiform canine of 50 individuals for determination of age via cementum annuli (Matson's Laboratory, Milltown, MT, USA—Boertje et al. 2015). In addition, we measured maximum rump fat depth for these 50 moose using a portable ultrasound device (Stephenson et al. 1998), and measured chest girth and body length (Hundertmark and Schwartz 1998). The ages of 13 additional moose were obtained from collared moose that died between the time of capture and data analysis, increasing the sample of known-aged moose to 63. Moose were captured and handled following protocols in accordance with applicable guidelines from the American Society of Mammalogists (Sikes et al. 2011) and approved by the Utah State University Institutional Animal Care and Use Committee (Protocol # IACUC-2365).

To determine whether each moose subsequently produced 1 or more calves, we conducted calf searches from the ground by locating each moose with telemetry during May and June. A moose was classified as non-parturient if it was not observed with a calf on multiple occasions in which observers had unobstructed views of the moose. Although effort was made to survey each moose during the peak calving period, because of logistical constraints it is likely some moose produced a calf that died before being surveyed. Therefore, calving rates should be considered minimum estimates. Surveys were conducted again the following March to estimate recruitment status for each animal known to have produced a calf. March recruitment surveys were conducted by locating radiocollared adult female moose from a helicopter and observing if calves were still present. Sample sizes differed among analyses based on available data.

Statistical analyses.—To determine whether mean maximum rump fat depths differed between moose with and without a calf at the time of capture, we used a nonparametric Wilcoxon rank sum test (Wilcoxon 1945) because rump fat data did not follow a normal distribution. We used generalized linear models (GLMs) to assess the relationship between rump fat depth (mm) in winter and pregnancy status at the time of capture, as well as subsequent parturition and calf recruitment. For the latter two analyses, only moose that tested positive for pregnancy at the time of capture were considered. Because reproduction in moose can be influenced by maternal age (Ericsson et al. 2001), we evaluated the effects of age in all models. Finally, because interpretation of rump fat can be confounded by the size of the animal, we converted the raw rump fat measurements to a scaled rump fat index using the equation developed by Cook et al. (2010). The scaled rump fat index accounts for differences in body size by using an allometric scaling equation where scaled rump fat = rump fat/0.15 x body mass$^{0.56}$ (Cook et al. 2010). Body mass for each moose was estimated using predictive equations from morphometric measurements taken at capture using equations predicting body mass from body length (Hundertmark and Schwartz 1998). The scaled rump fat index not only accounts for differences in body sizes among individuals within our sample, but also presents our data in a format that should allow valid comparisons to larger subspecies of moose. We used the scaled rump fat conversions for all models relating body fat to reproductive rates.

We used piecewise linear splines to test for nonlinear effects of rump fat on the probabilities of each metric of reproduction. Specifically, we tested for a threshold level

of rump fat beyond which the probability of reproduction abruptly changed. To determine the presence and position of fat-specific thresholds, we evaluated a set of competing GLMs. The set included models with a single knot placed at each integer from 1 to 8 mm, a model with no knot representing the hypothesis of no thresholds in reproductive rates, and an intercept-only model representing the null hypothesis that rump fat had no effect on reproduction. A knot was the join point between two linear splines. We selected knots *a priori* based on the prediction that reproductive rates should asymptote at high fat levels. Our placement of knots was consistent with guidelines for the efficient use of knots (Wold 1974; Eubanks 1984; Seber and Wild 2003). By definition, knots selected *a priori* are fixed (i.e. not random variables) and are therefore not estimated as parameters in models. We created variables containing a linear spline for rump fat depth with the MKSPLINE command in STATA 13.1 (StataCorp LP 2013). The variables were constructed so that the estimated coefficients measure the slopes of the segments before and after a given knot. We compared GLMs using Akaike's Information Criterion adjusted for small sample size (AIC_c—Burnham and Anderson 2002). In addition, we assessed whether including a variable for the presence of a calf at heel at the time of capture improved model fit by using likelihood ratio tests and associated $\chi 2$ values among nested models.

To compare the reproductive rates of moose in Utah with those of moose at higher latitudes in North America and to search for evidence of a possible range-limit effect in moose fecundity, we conducted a meta-analysis on pregnancy and twinning rates in moose. We constrained our literature review to studies that: 1) only considered animals ≥

2 years old (Boer 1992), 2) were conducted on free-ranging moose in North America, and 3) had a specific geographic location in which a latitude could be derived (i.e. not region-wide). Once moose reproductive rates were found that met these criteria, the latitude of the study area was either obtained from the text or was derived using the closest geographic feature to the center of the study area. Because moose have a circumpolar distribution, we considered high latitudes to be the range core and southern latitudes to represent the periphery or range limit. We included the method used for pregnancy or twinning determination as a categorical variable to account for potential variation arising due to the diagnostic method used. Following Schwartz (2007), methods of pregnancy determination included fetal counts which most often were conducted by examining reproductive tracts of dead moose, pregnancy-specific protein B (PSPB) from serum assays, progesterone from serum assays, fecal progesterone, or rectal palpation. Methods of twinning determination were either fetal counts or direct observations of numbers of juveniles per adult female conducted during the calving period. Twinning rates were defined as the percentage of parturient females that had 2 calves. For studies that presented both pregnancy and twinning rates over the same time period, we calculated a measure of fecundity by multiplying the pregnancy rate by litter size to estimate the expected number of young produced per adult female in each population. Because fecundity rates were composed of both pregnancy and twinning data, methods of fecundity determination were constructed as categorical variables with different combinations of twinning and pregnancy diagnostics respectively. We tested the hypothesis that moose reproductive rates declined with decreasing latitude (i.e. as the

population approached the southern range limit) using generalized linear mixed models (GLMMs) with a binomial distribution for pregnancy and twinning rate and a normal distribution for fecundity. Additionally, we included random intercept identifying the population. For studies that presented annual data on reproductive rates for more than 1 year, we retained each annual estimate in the analysis; the population-specific random intercept controlled for lack of independence between reproductive rates within the same population across multiple years. All analyses were performed in STATA 13.1 (StataCorp LP 2013).

RESULTS

Rump fat.—Rump fat depth of female moose (> 1 year old) in our study ranged from 0–21 mm (Fig. 2.1) with a mean ± *SE* of 4.5 ± 0.66 mm ($N = 50$). When converted to scaled rump fat to control for body size, scaled rump fat measurements averaged 5.0 ± 0.72 mm. Sixteen of 50 moose (32%) had a rump fat depth of 0 mm (Fig. 2.1). The presence of a calf at heel at the time of capture did not did not influence rump fat ($z = -0.19$, $P = 0.85$, $N = 50$); moose with calves at heel had a mean ± *SE* rump fat depth of 4.22 ± 0.81 mm ($N = 18$), and rump fat for those without calves measured 4.75 ± 0.94 mm ($N = 32$). When restricting this analysis to only prime-aged individuals (3.5–8.5 years old), moose with calves (3.71 mm ± 0.84, $N = 14$) had less rump fat than those without calves (7.39 mm ± 1.24, $N = 18$; $z = 2.12$, $P = 0.033$).

Pregnancy.—We acquired age-specific pregnancy rates for 63 moose > 1 year old (Fig. 2.2). Following the age classes defined by Boer (1992), yearling pregnancy rate was

0% (N = 5) and adult pregnancy rate was 74.1% (SE = 5.8%, N = 58). Nevertheless, classifying pregnancy rates into 3 age groups better highlighted the effects of age on pregnancy: moose 1.5–2.5 years old had low pregnancy rates (31.6%, SE = 10.9%, N =18), those between 3.5 and 8.5 years had high rates of pregnancy (91.9%, SE = 4.5%, N = 37), and individuals greater than 8.5 exhibited low pregnancy rates (37.5%, SE = 18.3%, N = 8). Hereafter, we used these breakpoints to classify each animal into 1 of 3 age classes: young (1.5–2.5 years old), prime (3.5–8.5 years old), and senescent (> 8.5 years old).

Calf production.—Of the females determined to be pregnant in winter 2013, 37% (25 of 67) were never seen with young at heel the subsequent spring. Although some calves likely died shortly after birth and before they could be surveyed, the large discrepancy between pregnancy rate and calving rate suggests at least some in-utero fetal losses occurred. Parturition rates among all moose (i.e. regardless of pregnancy status) varied from 44% (43 of 98) in 2013, 42% (28 of 67) in 2014, and 60% (29 of 47) in 2015. Twinning rates varied from 5% (2 sets of twins of 43 parturient females) in 2013, 4% (1 of 28) in 2014, and 0% (0 of 28) in 2015. Over the 3 years of the study, parturition rates averaged 47% (SE = 3.4%, N = 212) and twinning rates averaged 3% (SE = 1.7%, N = 100).

Rump fat and reproductive rates.—We modeled the probability of pregnancy as a function of rump fat for 50 moose for which data were available. The most parsimonious model included age and a linear spline for rump fat, indicating a threshold beyond which the effect of rump fat on pregnancy changed abruptly (Fig. 2.1; Table B.1). Evidence for

a model describing a linear relationship between rump fat and pregnancy had considerably less support ($\Delta AIC_c = 4.23$; Table B.1). The best-fit model included a threshold at 2 mm of rump fat (Table 2.1) such that the probability of pregnancy increased from 0 to 2 mm of rump fat but beyond this threshold there was no further change in the odds of pregnancy (Fig. 2.3a). Models with breakpoints located at 1, 3, 4 or 5 mm of rump fat also had substantial support ($\Delta AIC_c \leq 1.98$; Table B.1). The combined model weight for the top models (i.e. those which included a breakpoint between 1–5 mm of rump fat) was 0.77. Age had a significant effect on pregnancy, but only in the prime-age category ($P = 0.021$) with respect to the young category. A variable indicating the presence of a calf at heel at the time of capture was not significant ($P = 0.187$) and including this variable failed to improve model fit ($\chi^2_1 = 2.14$, $P = 0.143$). The final model predicted a 0.95 probability of pregnancy for moose with 2 mm of rump fat.

We surveyed 29 moose during May and June that tested positive for pregnancy and for which we had age and rump fat data. In contrast to the pregnancy model, the most parsimonious model describing the probability that pregnant moose produced young included only a linear term for rump fat. The probability of producing one or more calves increased linearly with rump fat ($P = 0.08$) with no apparent thresholds (Fig. 2.3b). Adult female age was not included the top model (Table B.2).

Additionally, we surveyed 21 moose the following March that tested positive for pregnancy and for which we had age and rump fat data. Similar to the parturition model, the best model describing the probability that pregnant moose recruited young until the following March included only rump fat which was positively related to recruitment ($P =$

0.05; Fig. 2.3c). Age and nonlinear terms for rump fat were not included in the most parsimonious model (Table B.3).

Reproductive rates and latitude.—For our meta-analysis, 39 studies reporting 76 pregnancy rates (Table B.4) and 50 studies reporting 117 twinning rates (Table B.5) satisfied the criteria for our review. Latitude was a significant parameter in both pregnancy ($P < 0.001$) and twinning models ($P = 0.001$); as populations increased in latitude, reproductive rates also tended to increase (Fig. 2.4a, b; Table 2.2). The odds of pregnancy and twinning changed at nearly the same rate with changes in latitude (*Odds Ratio* = 1.059 and 1.058, respectively). The analytical or field technique of determining pregnancy and twinning rates across studies was not an important predictor in either model ($P \geq 0.17$ and $P = 0.34$ for pregnancy and twinning rate determination methods, respectively; Table 2.2). Nevertheless, there was substantial, unexplained variation in both pregnancy and twining rates indicating unmeasured factors were important (Fig. 2.4a, b). The average pregnancy rate of all studies in our review was 85.0% ($N = 39$; $SE = 1.3\%$) and average twinning rate was 27.4% ($N = 51$; $SE = 2.4\%$)

For studies that presented data on both pregnancy and twinning rates over the same time period (29 studies reporting 48 annual estimates), we calculated fecundity which we defined as the expected number of young produced per adult female in each population. Fecundity tended to be higher for more northerly populations and exhibited a significant association with latitude ($P < 0.001$; Fig. 2.4c; Table 2.2). In this model, there was significant variation between certain methods used to diagnose reproductive rates (Table 2.2). Specifically, fecundity rates estimated from direct observation/fetal counts

and direct observation/fecal progesterone methods were significantly lower than the reference group direct observation/PSPB ($P \leq 0.001$), but other methods did not differ ($P \geq 0.09$; Table 2.2). After controlling for diagnostic method and including a population-specific random intercept, the model predicted that each 1 degree increase in latitude corresponded to 0.016 (95% *CI* = 0.008–0.024) additional young produced per adult female. Therefore, the northernmost population was expected to produce 0.48 additional young per adult female than in the southernmost population (i.e. Utah).

DISCUSSION

As with other subspecies of moose, reproductive success in Shiras moose was related to maternal fat stores (Heard et al. 1997; Testa and Adams 1998; Keech et al. 2000; White et al. 2014). Even though breeding had occurred several months before we measured rump fat, there was still a clear association between rump fat and pregnancy status. Similarly, the amount of midwinter fat stores was predictive of whether pregnant moose would eventually produce young, and recruit young until the following spring. Although a low threshold of rump fat during midwinter was predictive of pregnancy status, once pregnant, having more rump fat increased the probability of successfully producing and rearing viable offspring. Therefore, this pattern suggests that to become pregnant only low quantities of stored energy were required, but those with greater fat stores had increased success in future rearing of offspring. Likewise, Testa and Adams (1998) reported an asymptote in the amount of rump fat required for pregnancy, but a linear pattern between rump fat and parturition and survival of young in Alaskan moose.

Milner et al. (2013) suggested that moose could conceive even in poor body condition but may terminate pregnancies if winter conditions became limiting. Adult females could therefore postpone making the decision to skip reproduction until winter conditions were known; such an occurrence may partially explain the pattern we observed.

In accordance with other studies (Sand 1996; Heard et al. 1997; Ericsson et al. 2001), maternal age was an important determinant of pregnancy rates in moose, with both young and old age classes having lower pregnancy than prime-aged moose (Fig. 2.2). Although it is possible for yearling moose to become pregnant (Schwartz and Hundertmark 1993), none of the 5 yearlings in our study were pregnant. Because reproducing is more costly to younger moose which may encounter a tradeoff between reproduction and growth (Sæther and Heim 1993; Sand 1996), our results suggest that yearling moose in our study avoided reproducing in favor of growth. Moose > 9 years old in our sample had lower pregnancy rates than prime-aged individuals, although our sample contained few moose in the old age category. In contrast to the influence of age on pregnancy, age appeared to be a less important factor in determining calving or recruitment success, although our analyses were limited by sample size for moose of older ages.

Moose in our study population in Utah, USA had scaled rump fat depths in midwinter of 5.0 mm, and roughly 1/3 had no measurable rump fat. Until more comparisons can be made with other Shiras moose populations, it is unclear to what extent this fat level suggests nutritional limitation. In ungulates, fat stored in the rump region is among the last of subcutaneous fat reserves to deplete (Cook et al. 2010);

however, moose with no measurable rump fat can still possess between 0 and 5.6% ingesta-free body fat (IFBF; Stephenson et al. 1998). Therefore, data from moose that had no measureable rump fat inherently lack resolution and cannot precisely predict percent body fat. We therefore consider rump fat to be a simple but imperfect index of body condition and caution that the animals with no measurable rump fat are not directly comparable to one another. Although there are currently no methods to estimate IFBF in moose without measurable rump fat (Cook et al. 2010), our analyses suggest that the threshold in rump fat for mid-winter pregnancy is above the point in which subcutaneous fat reserves have been depleted.

Because our rump fat measurements were collected during January and February, they represent the nutritional state of animals near the midpoint between conception and parturition. However, the timing of measurements did not represent the peak nutritional state of an animal (i.e. autumn) and consequently, certain findings may require a nuanced interpretation. For example, we found no overall statistical difference in rump fat between adult females with and without calves at the time of handling. Logically, moose with calves would likely lose fat more rapidly than moose without calves due to the energetic demands of lactation. Due to differences in metabolic rates between moose with and without calves, by midwinter any differences in rump fat between groups may have been obscured. Nonetheless, our findings suggest that rump fat measured midwinter can still be valuable in terms of explaining variation in reproductive success.

Reproductive rates for adult moose tended to be lower as populations approached the southern range limit, although there was much variation in those trends. Latitude *per*

se likely has no effect on reproductive rates of moose, but instead reflects other factors that vary with latitude; e.g., climate, density dependence, primary productivity, genetics, or predation pressure. Regardless of latitude, a qualitative assessment suggests populations situated at the extreme southern range limit have below-average adult pregnancy rates: Utah (74%–this study), SW Wyoming (69%–K.L. Monteith and M.J. Kauffman, pers. comm.), NW Minnesota (48% including yearlings–Murray et al. 2006), NE Minnesota (75%–Severud et al. 2015), Michigan (74%–Dodge et al. 2004), New Hampshire (78%–Musante et al. 2010), and New Brunswick (79%–Boer 1987). This is consistent with biogeographic models suggesting that edge populations may have compromised fitness.

It has been suggested that moose can maintain relatively-high pregnancy rates despite environmental variation but will instead decrease litter size in response to declining nutrition (Gasaway et al. 1992; Gingras et al. 2014). Therefore, the product of pregnancy rate and litter size may be more confirmatory in determining if southern moose indeed are less productive. Our review of moose fecundity across North America (calculated from studies presenting both pregnancy and twinning rates) also indicated a trend of fewer young per adult female in populations at lower latitudes.

Our evaluation cannot elucidate the mechanism underpinning lower reproductive rates among southern moose populations, but suggests an overarching and relevant pattern. Fecundity in moose has often been attributed to habitat quality (Franzmann and Schwartz 1985; Gingras et al. 2014), because like other temperate ungulates, moose are capital breeders and rely partially on somatic reserves to support the demands associated

with reproduction. Consequently, reproductive rates should reflect habitat quality. At high latitudes the characteristics of the summer growing season allow for the production of higher quality forage for moose (Sand et al. 1995; Langvatn et al. 1996; Herfindal et al. 2006); therefore, it is possible that the latitudinal gradient in reproductive gradients we observed was caused by a north-south gradient in forage quality. This hypothesis is in accordance with the environmental gradient theory which predicts that habitat quality becomes marginal at range edges, often leading to lower population performance (Caughley et al. 1988; Talley 2007; Sexton et al. 2009). Further, cold-adapted species at their equatorial range limit may be even more susceptible to nutritional limitation when potential for thermal stress is considered (Monteith et al. 2015). Nevertheless, the large amount of variation in our data, regardless of the latitudinal position of the population, indicates that other local factors associated with environmental characteristics or other external factors are also important (Talley 2007; Sexton et al. 2009).

Alternatively, if southern moose populations occur at higher densities relative to their carrying capacity than more northerly populations (Peek 1974; Post 2005), nutritional limitation may be heightened by density dependence feedbacks. Monteith et al. (2015) suggested that recently-established moose populations in the U.S. Rocky Mountains have experienced irruptive population growth and some could be in excess of carrying capacity. Furthermore, in many southern moose populations including Utah, wolves (*Canis lupus*) and grizzly bears (*Ursus arctos*) have been extirpated and consequently, moose are not limited by these predators. As such, lower predation on

southern moose populations may allow them to reach higher densities than in more predator-abundant northern areas (Wang et al. 2009).

Reproductive rates for Shiras moose in our review were consistently low when compared to other subspecies, which accords with early researchers who postulated such an effect could be intrinsic to the subspecies (Houston 1968; Stevens 1970; Peek 1974). In particular, Shiras moose have among the lowest twinning rates in our review (Fig. 2.4b). Testa and Adams (1998) did not detect an effect of maternal body condition on the probability of twinning in moose, and instead proposed that phenotypic traits such as age and body size may be related to instances of twinning. Others, however, have reported maternal body mass was associated positively with production of twins (Schwartz and Hundertmark 1993; Sand 1996). Because Shiras moose are smaller bodied than other North American subspecies (Bubenik 2007), it is possible that twinning rates of Shiras moose are inherently limited by body size, and body size itself may be driven by either environmental or genetic differences among southern and northern populations (Herfindal et al. 2014).

Finally, decreased productivity of southern moose populations may represent the evolution of a reproductive strategy that maximizes individual fitness in response to local environmental characteristics (Araújo et al. 2015). Importantly, juvenile survival may be higher in moose populations nearest the equatorial range limit (Ferguson 2002). Because winter severity increases juvenile mortality in moose (Thompson 1980; Keech et al. 2000; Siversten et al. 2012), as environments become less seasonal in southerly latitudes, calf survival rates generally increase (Sand 1996; Ferguson 2002). Additionally, in

southern regions where wolves and grizzly bears are absent, young moose may be less at risk to predation than in predator abundant areas in the north. Therefore, lower productivity in southern moose may be offset by an increase in juvenile survival, and consequently may not depress population growth. If calf survival rates are indeed higher for southern moose, there may be little motivation for female moose to invest in larger litter sizes but instead allocate their available resources into a single calf with high odds of survival. Therefore, southern moose could optimize fitness by trading additional offspring for a higher probability of survival of a singleton—a potential form of conservative bet-hedging (Olofsson et al. 2009).

Our results suggest that demographic rates of moose can vary along geographic gradients, even for pregnancy rate which previously has been considered invariable and robust to environmental conditions (Boer 1992). We also documented the important role of maternal body fat in reproductive success in Shiras moose. These findings suggest that southern moose populations may be demographically vulnerable in terms of reproduction, particularly if future environmental conditions exacerbate foraging conditions which could result in decreases in production of young.

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TABLE 2.1.—Parameter estimates for the best-performing generalized linear model predicting reproductive rates as a function of scaled rump fat and age for a moose population sampled in northern Utah in 2013. Age was constructed as a categorical variable describing the age class of each moose; coefficients for this variable are given with respect to the young age category. The sample sizes were 50, 29, and 21 for pregnancy, parturition, and recruitment, respectively. Only moose that were determined to be pregnant in winter 2013 were included in analyses for parturition and recruitment.

						95% *CI*	
Response Variable	**Parameter**	**Estimate**	***SE***	***z***	***P***	**Lower**	**Upper**
Pregnancy	Rump fat ≤ 2 mm	2.07	0.81	2.55	0.01	0.48	3.66
	Rump fat > 2 mm	-0.11	0.16	-0.64	0.52	-0.43	0.22
	Age (Prime)	2.44	1.03	2.36	0.02	0.42	4.47
	Age (Senescent)	-1.57	1.78	-0.88	0.38	-5.06	1.92
	Intercept	-2.02	0.87	-2.34	0.02	-3.72	-0.33
Parturition	Rump fat (mm)	0.25	0.14	1.75	0.08	-0.03	0.53
	Intercept	-0.25	0.74	-0.33	0.74	-1.70	1.21
Recruitment	Rump fat (mm)	0.33	0.17	1.98	0.05	0.04	0.66
	Intercept	-1.26	0.89	-1.42	0.15	-3.00	0.48

TABLE 2.2.—Parameter estimates for generalized linear mixed models predicting reproductive rates in North American moose populations as a function of the latitude of each population and a categorical variable indicating the method of diagnosing reproductive rates. Methods of pregnancy rate determination were: FC = fetal count, FP = fecal progesterone, PR = progesterone, RP = rectal palpitation and PSPB = pregnancy-specific protein B (reference group). Methods of twinning rate determination were: DO = direct observation and FC (reference group). Fecundity rate was calculated as the product of pregnancy rate and twinning rate; thus, methods of determination included combinations of methods used in determining both pregnancy and twinning rates; the reference group for fecundity was DO/ PSPB.

						95% *CI*	
Response Variable	**Parameter**	**Estimate**	***SE***	***z***	***P***	**Lower**	**Upper**
Pregnancy	Latitude	0.057	0.013	4.45	<0.001	0.321	0.083
	FC	-0.154	0.19	-0.81	0.418	-0.527	0.219
	FP	-0.221	0.356	-0.62	0.536	-0.919	0.478
	PR	-0.416	0.359	-1.16	0.246	-1.119	0.287
	RP	-0.423	0.305	-1.38	0.167	-1.022	0.176
	Intercept	-1.134	0.649	-1.75	0.081	-2.406	0.138
Twinning	Latitude	0.057	0.017	3.26	0.001	0.023	0.091
	DO	-0.297	0.309	-0.96	0.336	-0.902	0.308
	Intercept	-4.123	0.944	-4.37	<0.001	-5.974	-2.271
Fecundity	Latitude	0.016	0.004	3.89	<0.001	0.008	0.024
	DO/FP	-0.215	0.0001	-224.2	<0.001	-0.215	-0.215
	DO/FC	-0.268	0.081	-3.29	0.001	-0.427	-0.108
	DO/RP	-0.046	0.095	-0.48	0.63	-0.232	0.14

FC/PSPB	-0.11	0.065	-1.66	0.096	-0.237	0.019
Intercept	0.277	0.193	1.44	0.15	-0.1	0.655

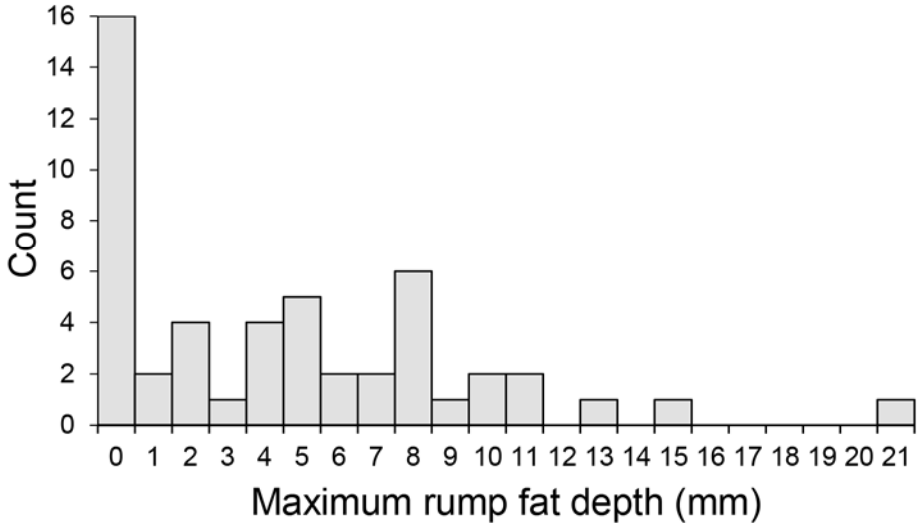

FIG. 2.1.—Frequencies of rump fat depths (unscaled) for 50 adult female moose measured in northern Utah, January-February 2013.

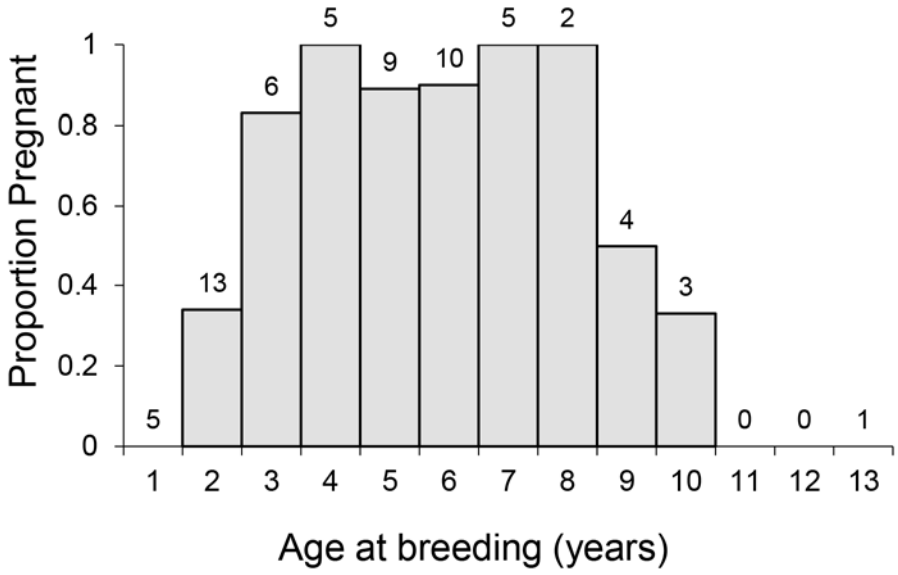

FIG. 2.2.—The proportion of adult female moose pregnant by age ($N = 63$) as determined by the pregnancy-specific protein B (PSPB) in January and February 2013. Sample sizes for each age are given above each column.

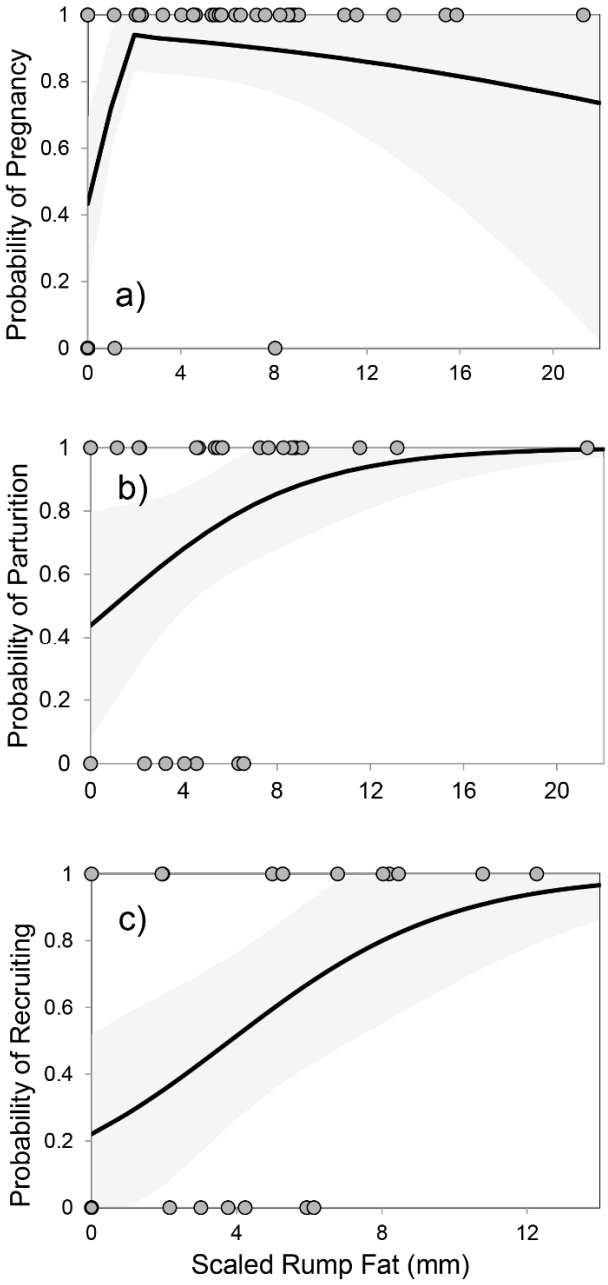

FIG. 2.3.—The predicted relationships between scaled winter rump fat depths and the probability of a) pregnancy ($N = 50$), b) parturition among pregnant females ($N = 29$), and c) recruitment of a calf until March ($N = 21$) for moose in northern Utah in 2013. Solid lines show the model predictions of reproductive success at various levels of rump fat and the 95% confidence interval of the prediction is given by the shaded region. Observed data points are indicated by gray circles.

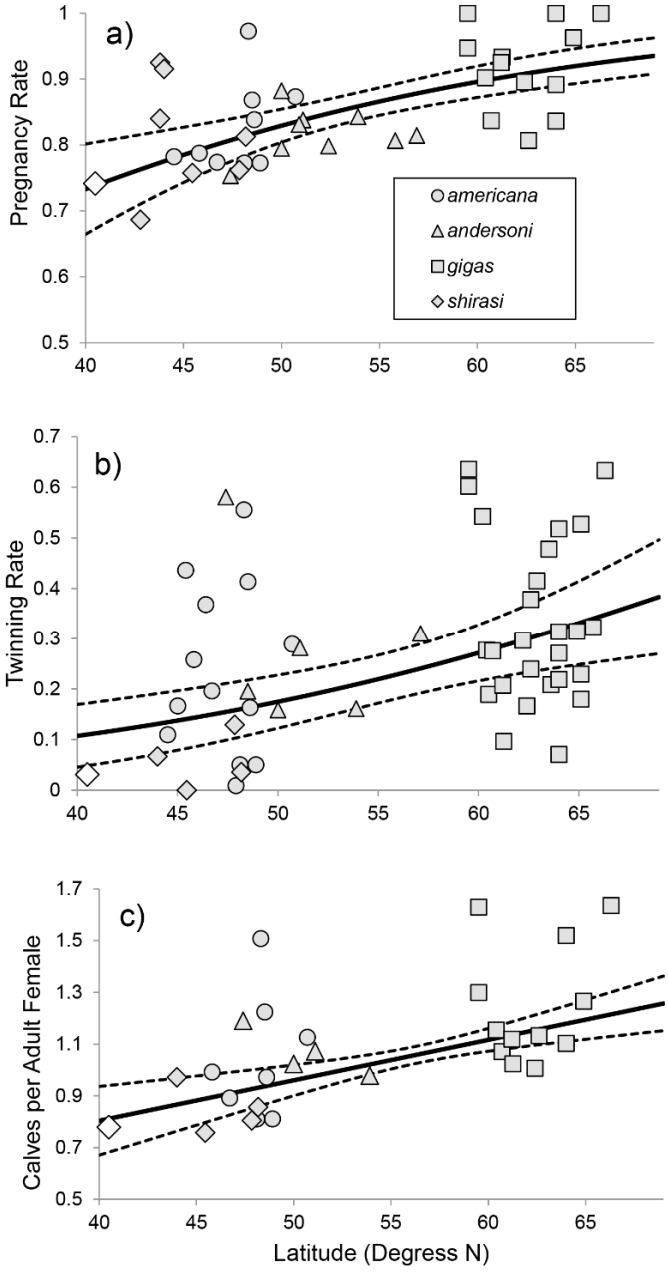

FIG. 2.4.—The relationships between latitude and a) pregnancy rate, b) twinning rate, and c) fecundity for adult female moose in various populations across their North American distribution. Observed proportions of reproductive rates among populations of different subspecies are represented by gray symbols, the prediction of reproduction rates as a function of latitude is given by the solid line, and the 95% confidence interval of the fitted line is given by dotted lines. Datapoints corresponding to the Utah population are given by white symbols.

CHAPTER 3

THE EFFECT OF CLIMATE ON POPULATION GROWTH IN A COLD-ADAPTED UNGULATE AT ITS EQUATORIAL RANGE LIMIT

Summary

1. Climatic changes are affecting the distribution and viability of species worldwide, and the effects may be greatest for heat-sensitive organisms in populations situated near the species' equatorial range limit.
2. We studied the population dynamics of a cold-adapted large herbivore, moose (*Alces alces shirasi*), in a population located at the extreme southern range limit in Utah, USA using a long-term dataset of counts conducted between 1958 and 2013.
3. In accordance with global patterns in which warming temperatures are affecting the dynamics of many species, we found that the population growth rate in this moose population was most sensitive to warm temperatures. Specifically, the lagged effects of maximum winter temperatures negatively affected population growth rates (β = -0.061, 95% Bayesian Credible Interval = -0.109, -0.014). However, the effects of population density and hunter harvest also showed the potential to limit population growth.
4. Based on model projections of moose abundance using composite effects of climate under 2 different future climate scenarios, the short term viability of this population does not appear at risk at conservative harvest levels. However, future

increases in winter temperatures are likely in this region, which increases the probability of population declines in the long term.

Introduction

Recent studies provide compelling evidence that climatic changes are affecting the distribution and viability of species across a diverse set of taxonomic groups worldwide (Bellard *et al.* 2012). Meta-analyses suggest that species in the northern hemisphere have experienced median decadal range shifts of 17 km northward and 11 m higher in elevation (Chen *et al.* 2011) indicating that populations at the southern range periphery are at high risk from environmental stress. Because of such tangible evidence of the effects of climatic changes, there is an increasing demand for biologists to anticipate the responses of species to future environmental change (Humphries, Umbanhowar & McCann 2004). However, there is incredible variation in taxonomic-specific responses to climatic change (Pearce-Higgins *et al*. 2015). This is partly because the effects of climate can affect organisms through different pathways: either by directly affecting individual physiological processes, or indirectly through changes in ecosystem processes (Stenseth *et al.* 2002). Consequently, the effects arising from either pathway may largely depend on the life history details of the organism (Chen *et al.* 2011).

For example, population dynamics of ungulates living in seasonal environments have evolved an intricate relationship with climate (Coulson, Milner-Gulland & Clutton-Brock 2000; Forchhammer *et al.* 2002; Post & Forchhammer 2002), and empirical evidence supports both direct and indirect climate effects. Direct (i.e. individual-level) influences of warming temperatures have caused individuals of various large herbivore

species to alter foraging strategies in response to high ambient temperatures (Owen-Smith 1998; Aublet *et al.* 2009), in some cases at the expense of lost body mass (van Beest & Milner 2013). Alternatively, indirect (i.e. ecosystem-level) effects arising from climatic changes have created mismatches between timing of reproduction and energy balance stemming from phenological advancement of vegetation growth (Post & Forchhammer 2008; Moyes *et al.* 2011). Another layer of complexity is added when indirect effects of climate influence competition for limited resources and the effects of population density become important. Typically, when climate mediates resource limitation, the effects are most apparent when population density is high (Bonenfant *et al.* 2009). Because of these nuances, the effects of climate on ungulates can be difficult to predict. Even within a particular species, populations in distinct environments can experience opposite responses to the same climate variable (Grøtan *et al.* 2009). This would especially hold true if the local climates differed between populations with respect to some species-specific optimum.

Moose (*Alces alces*) are a species which have evolved specific climatic tolerances, favoring cool and wet environments (Kelsall & Telfer 1974; Renecker & Hudson 1986). However, moose in North America occupy a large geographical region spanning > 30° latitude and in which the climate varies dramatically (Telfer 1984). Nonetheless, measures of demographic performance in moose often relate positively with precipitation (Thompson 1980; Murray *et al.* 2006; Monteith *et al.* 2015) and negatively with warm-season temperatures (Crete & Courtois 1997; Murray *et al.* 2006; Grøtan *et al*. 2009) across their distribution. The effects of winter climatic conditions, however, are

more inconsistent. In the northern parts of their distribution, severe winters are limiting to moose (Thompson 1980; Crete & Courtois 1997; Keech *et al.* 2000; Siversten, Mysterud & Gundersen 2012). Conversely, a southern-edge population in Minnesota has shown just the opposite—that warm winter temperatures negatively affect moose survival (Lenarz *et al.* 2009). Additionally, Monteith *et al.* (2015) showed that warmer annual temperatures tended to lower subsequent recruitment rates of southern moose populations in the intermountain west.

Therefore, moose populations located along the species' southern range limit offer a unique case study to investigate the effects of climate on peripheral populations of a cold-adapted species. In accordance with global patterns of climate-induced changes (Chen *et al.* 2011), moose populations along the southern range limit in certain parts of the United States have experienced drastic declines in recent decades thought to be at least partly due to climatic changes (Murray *et al.* 2006; Lenarz *et al.* 2009; Lenarz *et al.* 2010). But curiously, in the last century moose in the western United States have naturally colonized new areas farther south than what is believed to be their historic range in spite of warming temperatures (Darimont *et al.* 2005; Wolfe, Hersey & Stoner 2010). Although many of these recently-colonized populations experienced phases of rapid growth after exploiting new habitats, many have since stabilized or begun to decline (Monteith *et al.* 2015). Thus, the long-term viability of these recently-established populations at the species' southern range limit is not known.

Although previous studies assessing the vulnerability of southern moose populations to climate are significant contributions (Lenarz *et al.* 2009; Monteith *et al.*

2015), as with all studies, they have limitations. First, the results of Lenarz *et al.* (2009) have recently been called into question due to the small sample size of annual survival rates ($N = 6$) used in that study (Mech & Fieberg 2014). Mech & Fieberg (2014) suggested that predation by wolves accounted for more moose mortalities than previously thought and that the negative effect of January temperature may have been overstated. Although Monteith *et al.* (2015) used data spanning a long temporal period and across a larger geographical area, both studies only measured a single fitness component. And importantly, neither study was able to account for the effects of population density, so it remains unclear as to if the climatic effects were density dependent. Therefore, although there is a growing body of evidence that southern moose populations are limited by warm winter temperatures, more support is necessary before the pattern can be generalized.

In contrast to studying a single fitness component, population growth rate is an omnibus measure of population dynamics because it accounts for the realizations of all demographic processes. For that reason, population growth rate has been suggested as the best response variable for analyzing population dynamics (Sibly & Hone 2002). When longitudinal count data are available, population growth rate can be estimated and analyzed to determine the effect of climate variables (Vucetich & Peterson 2004; Forchhammer *et al*. 2002). A particularly attractive approach is when count data are formulated as a state-space model (Buckland *et al*. 2004; Clark & Bjørnstad 2004), thereby separating the ecological signature of the time series from observation error which is pervasive in many datasets of free-ranging animals. Such models can also easily be formulated to measure the effect of density dependence (Dennis *et al*. 2006). In

addition, by implementing an interaction effect between population density and climate, inference could be drawn regarding whether the effect of climate occurs at equal magnitude across population densities, or whether the climate variable affects the population more strongly at high densities (Hobbs & Hooten 2015). If such an interaction suggested that the magnitude of the climate variable is strongest at high population densities, this would provide evidence that the climate variable operated according to a density-dependent mechanism. If no interaction effects were evident, then more evidence could be placed on a direct mechanism related to measures of physiological well-being, such as those arising from the effects of heat stress.

Here, we use count data spanning 56 years to test hypotheses related to the influence of climate and population density on the growth rates of a harvested moose population in Utah that occurs at the species' extreme southern range limit. We hypothesized that 1) population growth rate would be density-dependent; i.e. that higher population density would act to slow population growth, and 2) because the population occurs at the southern edge of moose distribution, dry and warm climatic conditions 1-2 years preceding surveys would also negatively influence population growth. We then assessed the support for interactions between population density and the climate variable found to best describe variation in population growth in order to assess whether the climate predictor influenced moose in a density-dependent or density-independent fashion. Finally, based on our best model describing population growth, we used data from the World Climate Research Programme to forecast the short-term trends in moose abundance under various scenarios of harvest rate. By quantifying the effects of harvest,

climate, and population density of moose in Utah, we hope to provide robust inference to best manage for the persistence of this heat-sensitive ungulate in a warming climate.

Materials and Methods

DATA

The Utah Division of Wildlife Resources (UDWR) began conducting winter aerial surveys to obtain minimum statewide abundances of big game beginning in 1958. At that time moose had only recently colonized the state and were only thought to be present in one management unit. Over time, moose expanded into neighboring management units, and presently occupy 10 management units in the northeast part of the state (Fig. 3.1). Early on, surveys were conducted using fixed-wing aircraft but since 1963 have been conducted using helicopters. Initially, management units were surveyed every year, but later switched to an irregular rotation in which only a subset of units were surveyed each year conditional on good survey conditions, and each unit was surveyed on average every third year. All suitable habitat within each management unit was surveyed according to expert opinion of biologists and routes were flown as consistently as possible between years. Moose were classified by sex and age-class (calf or adult) but in this study we only considered total individuals regardless of sex or age. Wolfe, Hersey & Stoner (2010) provide more details on survey methodology.

MODEL SPECIFICATION

Our survey data are inherently biased low due to the difficulty of observing every animal on the landscape. Because survey data were not sightability-corrected and

represent only minimum counts, our models do not predict true population abundances but instead provide a population index on the same scale as the raw counts. However, because survey methodology has been relatively consistent over time, it is valid to model minimum counts as representation of true population dynamics (Kery & Schaub 2012). Additionally, the periodic nature of the surveys meant that missing data-years were common. To accommodate these issues, we implemented state-space models which have the ability to separate noise arising from biological processes from that which arises from random under- and over-counting (Buckland *et al.* 2004; Dennis *et al*. 2006); hereafter "process error" or "observation error," respectively. Although state-space models can be implemented using both frequentist and Bayesian approaches, we opted to use Bayesian models because of the ease in which they can accommodate missing data (Kery & Schaub 2012).

We used the Gompertz population growth model (equation 1) because it has been widely used in state-space models of time series of animal counts and exhibits several desirable qualities. First, it has the ability to estimate the strength of density dependence (denoted β_1 in the equation), by integrating an autoregressive term relating population abundance in the present year (N_t) to the previous year's count (N_{t-1}). When $\beta_1 < 0$, population density exhibits a negative effect on population growth; when $\beta_1 > 0$ population density positively affects population growth (i.e. an Allee effect), and when $\beta_1 = 0$, density independence is assumed (Dennis *et al*. 2006). Because moose densities and the time since establishment were variable across survey units, we estimated a unique β_1 parameter for each management unit, i.e. a group-level effect. The parameter r_{max} (β_0 in

the equations) is estimated from the model and is equivalent to the maximum intrinsic rate of increase (Dennis *et al*. 2006), i.e. the maximum growth rate a given species could attain if resources were unlimited (Hone, Duncan & Forsyth 2010). The raw counts are represented by Y and the population estimates are denoted by N. The model is indexed by the subscript i representing each of the 10 management units in which surveys were conducted, and the subscript t denoting each of the 56 years during which surveys were conducted (1958-2013).

Because a portion of moose in northern Utah are harvested annually and the UDWR requires mandatory harvest reports to be submitted for moose, we added a term in the model to account for known annual harvests of moose (both bull and cow harvest combined; equation 2). This adds realism to the model by moderating the number of moose counted at N_t to include the number of moose known to be harvested in the previous year (Colchero *et al*. 2009; Koons *et al*. 2015). We then added the parameter β_2 to measure the effect of a climate variable, which completes the deterministic portion of the Gompertz model (equation 3). For shorthand, we refer to equation 3 as $g(N_{i,t-1})$. A lognormal error term (σ_p^2) estimates the process error, or error not explained by the deterministic portion of the Gompertz model (equation 4). The error arising from imperfect sampling, i.e., observation error, is accounted for by specifying that the count data $Y_{i,t}$ arose from a Poisson distribution with rate parameter equal to $N_{i,t-1}$ (equation 5). Finally, we summed the unit-level population indices at each time step to arrive at an index of the population-wide abundance (equation 6).

Equation 1:

$$N_t = N_{t-1} * e^{\left(\beta_0 + \beta_{1,i} * \log(N_{t-1})\right)}$$

Equation 2:

$$N_{i,t} = \left(N_{i,t-1} * e^{\left(\beta_0 + \beta_{1,i} * \log(N_{i,t-1})\right)}\right) - \text{Harvest}_{i,t-1}$$

Equation 3:

$$N_{i,t} = \left(N_{i,t-1} * e^{\left(\beta_0 + \beta_{1,i} * \log(N_{i,t-1}) + \beta_2 * \text{climate}_t\right)}\right) - \text{Harvest}_{i,t-1}$$

Equation 4:

$$N_{i,t} \sim \text{lognormal}\left(\log\left(g\left(N_{i,t-1}\right)\right), \sigma_p^2\right)$$

Equation 5:

$$Y_{i,t} \sim \text{Poisson}(N_{i,t})$$

Equation 6:

$$N_{\text{total},t} = \sum_{i=1}^{10} N_{i,t}$$

In Bayesian analyses, prior distributions must be provided for all random variables in the model. We chose vague priors for parameters for which we had no prior information, i.e., process error (σ_p^2) and the effect of climate (β_2). However, we used more informative priors for parameters which could be reliably estimated from ecological

theory, i.e., the strength of density dependence (β_1) and r_{max} in moose (β_0). We followed the approach of Koons *et al*. (2015) in defining a prior distribution for β_1 to exclude impossibilities of the effect of population density on growth rate in the Gompertz model (Dennis *et al*. 2006). Also following Koons *et al*. (2015), we estimated an informative prior for β_0 ($\bar{x}$ = 0.304, *SD* = 0.08) based on the mean of five previous studies which provided estimates of r_{max} in moose (Bergerud 1981; Keith 1983; Van Ballenberghe 1983; Cederlund & Sand 1991; Sinclair 2003). Informing the parameters in which reliable prior information can be obtained results in better identifiability of other model parameters such as the separation of process and observation error (Lebreton & Gimenez 2013; Koons *et al*. 2015).

A directed acyclic diagram of the model structure is provided as a visual aid in Appendix C (Fig. C.1). The full model, including prior distributions, is specified by the following statement, in which items in bold represent matrices:

$$\Pr\left[\boldsymbol{N}, \boldsymbol{\beta}, \sigma_p^2 \middle| Y_{i,t}, \text{harvest}_{i,t}\right] \propto$$

Process Model:

$$\prod_{i=1}^{10}\prod_{t=2}^{56} \text{lognormal}\left(N_{i,t} \middle| g\left(N_{i,t-1}; \boldsymbol{\beta}\right), \sigma_p^2\right) \times$$

Observation Model:

$$\prod_{i=1}^{10}\prod_{t=1}^{56}\text{Poisson}(Y_{i,t}\,|N_{i,t}) \times$$

Parameter Models:

$$\text{Uniform}(\sigma_p^2|0,\,2) \times$$

$$\text{Normal}(\beta_0|0.304,\;\; 0.08^2) \times$$

$$\text{Normal}\left(\beta_{1,i}\middle|0,2^2\right)\text{T}(-2,\,2) \times$$

$$\text{Normal}(\beta_2|0,10^2)$$

MODELLING APPROACH

We first acquired monthly temperature and precipitation data from the National Oceanic and Atmospheric Administration/National Climatic Data Center (NOAA/NCDC) nClimDiv dataset (Vose *et al*. 2014) the for the Utah Northern Mountains climate division, as well as monthly snow depth data from the United States Department of Agriculture (USDA) National Water and Climate Center. We then created seasonal variables for the following climate metrics we hypothesized could explain variation in moose population growth rates: maximum winter temperature, maximum spring temperature, maximum summer temperature, total spring precipitation, total summer precipitation, and average winter snow depth. We defined winter as January-March; spring as April- June; and summer as July-September. We considered each climate variable at lags of 1 and 2 years. Although aerial counts were conducted between

December and February according to good survey conditions, for consistency we assumed each count was conducted in January of year *t*; accordingly, any climate variable in the preceding 12 months would be defined as a lag of 1 year because it was a different calendar year. For example, for a count conducted in 2013, a winter variable with a lag of one year would correspond to climatic conditions between January and March of 2012. All climate variables were standardized to have *mean* = 0 and *SD* = 1 to assist in convergence and ease of interpretation. Thus, the coefficient estimates for univariate climate variables are on the same scale and directly comparable.

Because currently there is not an appropriate information criterion for Bayesian state-space models (Hooten & Hobbs 2015), model selection cannot be conducted using an Information-Theoretic approach as is typically implemented in frequentist analyses. Therefore, to determine the effects of the climate variables on population growth rate, we instead let each climate variable enter the model by itself and gauged its importance using probability (*P*) values. *P*-values were constructed by calculating the proportion of model iterations in which the variable has an effect consistent with the direction of the coefficient estimate. In other words, a variable with a positive coefficient and a *P*-value of 0.95 indicates that in 95% of the iterations, the variable's effect was positive. *P*-values can thus be interpreted as the weight of evidence in which the variable has a non-zero effect. Similarly, a 95% Bayesian Credible Interval (*BCI*) is the interval based on 95% of the highest posterior density for a given parameter. We considered our top model to be the model containing the highest-ranking climate variable.

After determining the individual climate variable which was most important in explaining variation in population growth rate, we then created an interaction term between the climate variable and population density. Strong support for an interaction term would suggest that the magnitude of the climate variable was influenced by population density, i.e., a density-dependent effect. In the previous univariate climate analyses each climate variable was scaled and centered; however, for the interaction between population abundance and climate it would be inappropriate to center the climate predictor without also centering the abundance estimate, which is not biologically reasonable. Therefore, for the interaction model, the climate variable was standardized to have $SD = 1$ but was not centered.

Finally, in order to project the effects of climate on future trends of moose abundance in our study area, we acquired climate forecast data for the variables found to be most important in explaining variation in moose population growth rate from the World Climate Research Programme's Coupled Model Intercomparison Project phase 5 (CMIP5) dataset. The CMIP5 dataset provides the most-current projections of climate arising from three emissions scenarios based on an ensemble of 16 core models (Maurer *et al*. 2007). Because these core models vary by region and climatic variable in their predictive ability, we acquired data from only those core models shown to perform with high accuracy in the region our study took place (Sheffield *et al*. 2013). We considered two sets of climate forecasts which differ according to future emission levels: Representative Concentration Pathway (RCP) 4.5 and RCP 8.5. RCP 4.5 is an optimistic

scenario which assumes reductions in emissions while RCP 8.5 is considered a "business as usual" (i.e. high) greenhouse gas emissions scenario (Riahi *et al*. 2011).

We hypothesized that various climate variables could have important effects and that projecting future moose abundance using univariate climate models may therefore be over simplistic. To consider composite effects of climate while maintaining model parsimony, we conducted principal component analysis to reduce the dimensionality of the most important climate variables. Specifically, we included all climate variables which had > 80% certainty of a non-zero effect from univariate climate models as inputs to the principal component analysis. We retained principal components which had eigenvalues > 1 and in which the variation accounted for was greater than that of a single climate variable considered separately. Using principal component loadings constructed from observed climate data, we predicted principal components of the future climate using forecasted climate data. The principal components should therefore retain important variation in climate while maintaining model parsimony. We then forecasted moose abundances until 2023 using principal components of climate as predictors, and evaluated the probability the population would experience growth by calculating the proportion of iterations in which the 2023 estimate was greater than the 2013 estimate (Kery & Schaub 2012).

MODEL IMPLEMENTATION

We conducted Markov Chain Monte Carlo (MCMC) simulations in JAGS (v. 3.4.0; Plummer 2012) via Program R and the R2jags package (Su & Yajima 2012) to estimate posterior distributions of the parameters of interest. For each model we ran three

chains each consisting of 100,000 iterations with the first 50,000 discarded as burn-in, and thinned the sample to retain every 50th simulation. Model convergence was assessed visually using traceplots and by ensuring each parameter of interest had a $\widehat{R}$ value < 1.1 (Gelman 1996). If models had not reached convergence after 100,000 iterations, we updated the model with additional iterations until convergence was satisfactory. We assessed model goodness-of-fit using posterior predictive checks (Gelman 2004; Kery & Schaub 2012; Hobbs & Hooten 2015). To do this, we generated hypothetical count data (i.e. $Y.new_{i,t}$) from the model and used a squared discrepancy statistic to compare observed and expected values from the original and new datasets at every MCMC iteration, i.e. $\left(Y_{i,t} - N_{i,t}\right)^2$ and $\left(Y.new_{i,t} - N_{i,t}\right)^2$, respectively. Calculating the proportion of iterations in which the discrepancy statistics arising from the original and hypothetical datasets are more extreme than one another provides a measure of goodness-of-fit; a value of 0.5 would indicate perfect fit, while values close to 0 or 1 suggest a lack-of-fit.

Results

None of the models we implemented suggested evidence of lack of fit from posterior predictive checks, i.e. values of posterior predictive checks were > 0.4 and < 0.6. Additionally, we only made inference on models which had successfully converged. When assessed individually, the climate variable with the strongest effect was winter maximum temperature$_{t-2}$ which had a negative effect on population growth rate (β_2 = -0.061). This variable had a high probability that the true effect was indeed negative (P = 0.995) and additionally, had a 95% *BCI* that did not overlap zero (-0.109, -0.014). The second highest ranked climate variable was spring temperature$_{t-1}$ which had a positive

effect on population growth rate (β_2 = -0.061), and also indicated strong evidence of a non-zero effect (P = 0.98) and in which the 95% *BCI* did not overlap zero (0.003, 0.113). The effects of summer precipitation at $year_{t-1}$ and $year_{t-2}$ also ranked highly and showed positive effects on population growth rate, but with less support (P = 0.943 and P = 0.935, respectively). The remaining climate variables had weaker and more variable effects (P < 0.92; Table 3.1). Because winter maximum $temperature_{t-2}$ was the highest ranking climate variable, we used the model containing that variable to make inference on the dynamics of the population (Table 3.2, Fig. 3.2).

To determine whether the highest-ranked climate variable acted in a density dependent or density independent fashion, we assessed the importance of winter maximum $temperature_{t-2}$ formulated as an interaction with population size (N_{t-1}). This interaction term exhibited strong support (P = 0.997) of a non-zero effect. The interaction suggested that the magnitude of the effect of winter temperature was strongest (i.e. most negative) in years when moose population density was high (β_{int} = -0.203; 95% *BCI* = -0.326, -0.062). At low population density, population growth rate (lambda) was > 1 regardless of winter climate (Fig. 3.3). However, as population size increased, the effect of winter temperature became pronounced, and warm winters quickly caused lambda to drop below 1. In contrast, in cool winters, the effect of population size had little effect on lambda.

For the highest ranking model, the coefficient estimates for β_1 were negative (Table 3.2) suggesting population growth rate was negatively affected by population size. Additionally, the 95% *BCI* for β_1 did not overlap zero in 8 of the 10 survey units,

providing strong support for the effect of density dependence in the majority of the units. The estimate of β_0 in the top model predicted an r_{max} of 0.269 (*SD* = 0.05; 95% *BCI* = 0.17-0.37) for this population.

Seven climate variables met our criteria of having > 80% confidence of a non-zero effect (Table 3.1) and were included in a principal component analysis to reduce the number of predictors used to forecast future population trends. The first three principal components (PCs) explained 62% of the variation among important climate variables, and by considering these three principal components we reduced the dimensionality of important climate predictors by 57%. PCs 4 and greater all had eigenvalues < 1 and explained less variation than if considered separately, so were not retained. PC 1 represented variation in spring climate in the year immediately preceding surveys; specifically, it related positively to spring maximum temperature$_{t-1}$ and negatively to spring precipitation$_{t-1}$. PC 2 predominantly reflected a positive relationship with winter maximum temperature$_{t-1}$, but also related positively to spring maximum temperature$_{t-2}$ and negatively to summer precipitation$_{t-2}$. PC 3 related negatively to winter maximum temperature$_{t-2}$ and to a lesser degree, spring maximum temperature$_{t-2}$.

After incorporating principal components from CMIP5-forecasted data into the model, our projections of moose abundance differed by both climate and harvest scenario (Fig. 3.4). At any given harvest rate, population growth was lower under the RCP 8.5 scenario than RCP 4.5. At harvest rates of 0–5%, both climate scenarios predicted growth would occur between 2013 and 2023 with probabilities ≥ 0.84. At a 10% harvest rate, both the RCP 4.5 and 8.5 scenarios still predicted growth, but with lower probabilities

(0.76 and 0.57, respectively). At a 15% harvest rate, both climate scenarios predicted population decline (Fig. 3.4).

Discussion

Our results support previous suggestions that warm winter temperatures negatively affect vital rates in southern moose populations (Lenarz *et al*. 2009). Although we are unable to determine the specific mechanism in which warm winter temperatures affect moose, we have evidence that the effect is density-dependent because of the strong support for an interaction between population density and winter temperature. While this does not preclude the possibility of direct heat stress affecting moose, if heat stress was responsible for directly killing moose due to exceeding physiological tolerances, we suggest the effect would operate on the individual level and would therefore be independent of population density. In addition, we believe such an effect would be most evident for winter conditions occurring in the year immediately preceding the count, not at a lag of 2 years as we observed.

Instead, we propose two possible pathways through which the negative effects of warm winter temperatures influenced population growth in our study. First, warm winters two years prior to our counts would correspond to favorable conditions for survival and reproduction of a common parasite of moose—winter ticks (*Dermacentor albipictus*). Winter tick abundances increase following warm late-winters when adult female ticks fall off their hosts and experience mild conditions allowing them to survive and reproduce (Drew & Samuel 1986; Garner & Wilton 1993; DelGiudice, Peterson & Samuel 1997; Samuel 2007). The following autumn would then be associated with a high abundance of

young ticks available to infect moose. Because the effects of tick infestations on moose are greatest at the end of winter (Samuel 2007), any tick-related die-offs in our study would not be apparent until the population was surveyed the following year. Hence, there would be a lag of two years between warm winter conditions and when a change in the population could be noted. Winter ticks have been a suspected limiting factor for moose in our study area (Wolfe, Hersey & Stoner 2010) as well as many other North American populations. Further, tick infestations are believed to be more severe when moose density is high (Samuel 2007), which is consistent with the interaction effect for which we found support. However, future studies would be required to confirm the extent to which ticks are responsible for the pattern we found.

Alternatively, warm winter conditions could influence subsequent foraging conditions because the phenology of spring green-up is largely controlled by late winter temperatures (Clark *et al*. 2014). There is much evidence that warming temperatures are associated with advances in spring green-up (Cleland *et al*. 2007). Consequently, an earlier onset of spring may be associated with a rapid green-up, ultimately shortening the period in which high quality forage is available. In turn, this may be associated with reduced reproductive output mediated by a change in maternal body condition (Monteith *et al*. 2015). Previous studies have found green-up conditions measured by NDVI have high explanatory power for metrics of moose demography (Brown 2011; Monteith *et al*. 2015); however, our count data preceded the timespan in which NDVI data are available so it was not possible to use as a covariate.

Spring maximum temperatures in the year immediately preceding surveys also importantly influenced population growth. In contrast to the negative effects of winter maximum temperatures$_{t-2}$, warmer springs related positively to population growth. If the negative impacts of winter maximum temperatures$_{t-2}$ affected moose due to high parasite loads, warm springs the next year could provide early foraging opportunities that could conceivably alleviate the effects of moose in poor condition from tick infestations. Spring temperatures are also predicted to increase in the future which, according to our model, may benefit moose in our study area. The extent to which rising temperatures will affect moose may therefore depend on whether winter or spring temperatures increase more quickly.

Also consistent with our hypothesis and in accordance with ecological theory is that as population density within each unit increased, population growth rate was dampened. This is a noteworthy finding given that direct evidence of density dependence can be difficult to detect in wild populations (Bonenfant *et al*. 2009). Moreover, the finding that density dependence is operating in this population is in accordance with the suggestion that Shiras moose populations in the Rocky Mountain states experienced irruptive population growth after exploiting novel habitats, and subsequently have undergone density-dependent oscillations in abundance around carrying capacity (Monteith *et al*. 2015). Our model supports this theory quantitatively, and additionally, a plot of our estimated abundances across time is qualitatively suggestive of this pattern (Fig. 3.2).

Our top model predicted an r_{max} value of 0.27, which was lower than the average r_{max} we estimated from other moose populations. While methods of estimating r_{max} vary (Hone, Duncan & Forsyth 2010), our results nonetheless suggest that the moose population in Utah may have a lower potential for growth than in other regions. Although some consider r_{max} to be an evolved trait which is intrinsic to the species and not affected by the environment (Street *et al*. 2015), our result agrees with the prediction by Caughley *et al*. (1988) in which r_{max} should decrease as populations approach the species' range limit and environmental stress becomes more limiting.

Our forecasts of moose abundance suggested that at conservative harvest rates, the short-term viability of Utah's moose population is probably not at great risk. However, the projected abundances were sensitive to the level of harvest, and annual harvest rates in excess of 10% predicted population declines. Additionally, future increases in winter temperature in this region are probable, which may further reduce the potential of future population growth regardless of harvest rates. Under all harvest scenarios, forecasts using RCP 8.5 data showed lower population growth than using RCP 4.5 data. Because the RCP 8.5 scenario is based on a scenario in which there is no change in greenhouse gas emissions, we believe this is a more realistic scenario given our short-term forecast horizon (i.e., a reduction in greenhouse gas emissions would be unlikely to occur by 2023). Our forecasts were intentionally limited in duration because of the difficulties in making precise long-term forecasts. Even in the 10 year span in which we made forecasts, there was high variation in the predictions as evidenced by the 95% *BCI* (Fig. 3.4). Thus, we suggest that managers continue to monitor this population with a

view that the dynamic effects of climate, population density, and harvest all have the potential to limit the population.

Why some southern moose populations have responded much more negatively to changes in climate than others remains unclear (Murray *et al*. 2012). In contrast to the drastic declines in moose abundance in Minnesota (Murray *et al*. 2006, Lenarz *et al*. 2009, Lenarz *et al*. 2010), moose in this study have largely remained stable at a statewide level. One possible explanation is that because Utah is topographically heterogeneous, the diversity in elevations may allow moose the flexibility to shift upward in altitude to cope with rising ambient temperatures. This pattern has been shown for another heat-sensitive mammal at its southern range limit, the American pika (*Ochotona princeps*; Ray, Beever & Loarie 2012). However, moose in areas such as Minnesota which have less-complex topographies may not have the option to shift upward in elevation and instead may be forced northward.

Broadly, our results support the global pattern in which northern-hemispheric species at their equatorial range limit show sensitivity to warming conditions. Although in the short term our results do not suggest an imminent northward range contraction of moose in Utah, we found a strong demographic response negatively related to warming winter temperatures. As future temperatures are predicted to increase over the next century, this finding may indicate an increased risk to the population in the future.

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Table 3.1. Parameter estimates for the effect of various climate variables on population growth rate of moose in Utah, 1958-2013.

Variable	**β Estimate**	**95% *BCI***	***P*(β ≠ 0)**
Winter max temp$_{t-2}$	-0.061	-0.109, -0.014	0.995
Spring max temp$_{t-1}$	0.057	0.003, 0.113	0.980
Summer precip $_{t-2}$	0.043	-0.011, 0.095	0.943
Summer precip $_{t-1}$	0.036	-0.010, 0.084	0.935
Spring precip $_{t-1}$	-0.048	-0.116, 0.020	0.917
Winter max temp $_{t-1}$	-0.034	-0.084, 0.017	0.907
Spring max temp $_{t-2}$	0.025	-0.026, 0.073	0.833
Summer max temp $_{t-1}$	0.019	-0.028, 0.065	0.787
Spring precip $_{t-2}$	-0.020	-0.072, 0.032	0.766
Summer max temp $_{t-1}$	0.016	-0.028, 0.062	0.756
Winter snow depth $_{t-2}$	0.008	-0.043, 0.060	0.630
Winter snow depth $_{t-1}$	0.004	-0.045, 0.054	0.571

Table 3.2. Parameter estimates for a model describing variation in population growth in moose in Utah, 1958-2013. β_0 is equivalent to r_{max}, β_1 describes the effect of density on population growth in each of 10 survey units, β_2 estimates the effect of winter maximum temperature$_{t-2}$ on population growth, and σ_p is process error.

Parameter	β Estimate	Standard Deviation	95% *BCI*
β_0	0.269	0.051	0.171, 0.37
$\beta_{1,1}$	-0.025	0.012	-0.05, -0.002
$\beta_{1,2}$	-0.031	0.018	-0.067, 0.001
$\beta_{1,3}$	-0.028	0.013	-0.053, -0.004
$\beta_{1,4}$	-0.029	0.013	-0.056, -0.003
$\beta_{1,5}$	-0.007	0.015	-0.037, 0.022
$\beta_{1,6}$	-0.028	0.013	-0.054, -0.003
$\beta_{1,7}$	-0.037	0.015	-0.066, -0.006
$\beta_{1,8}$	-0.052	0.018	-0.088, -0.017
$\beta_{1,9}$	-0.039	0.018	-0.073, -0.005
$\beta_{1,10}$	-0.035	0.014	-0.062, -0.007
β_2	-0.061	0.024	-0.108, -0.013
σ_p	0.311	0.024	0.268, 0.361

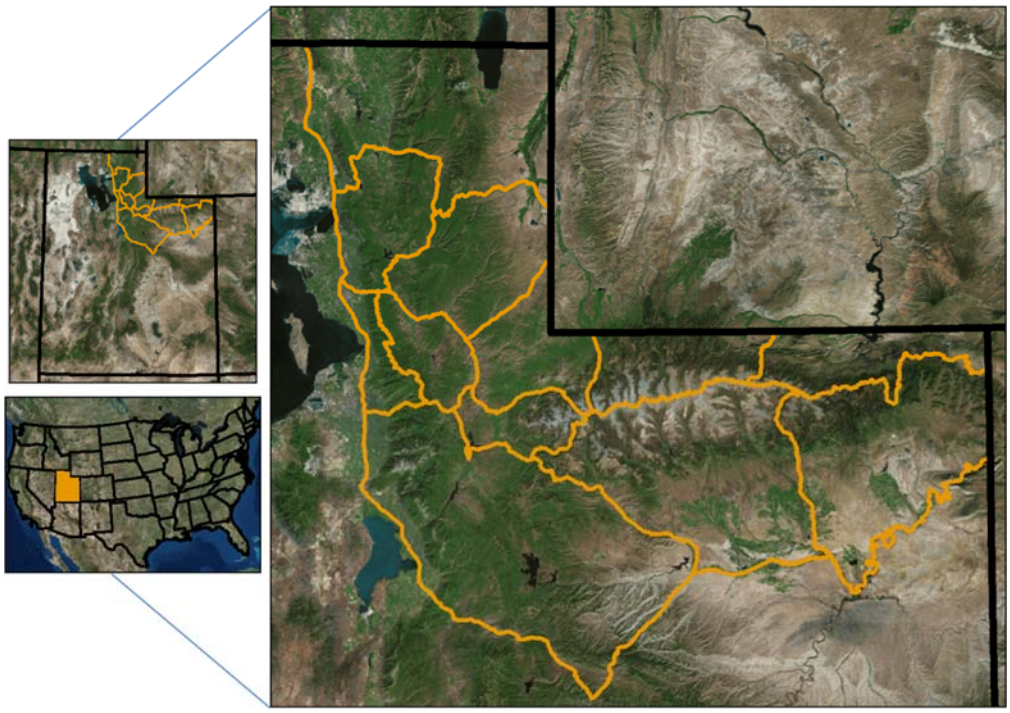

Fig. 3.1. Management units (orange outlines) in northeastern Utah, USA in which population counts of moose were conducted, 1958-2013.

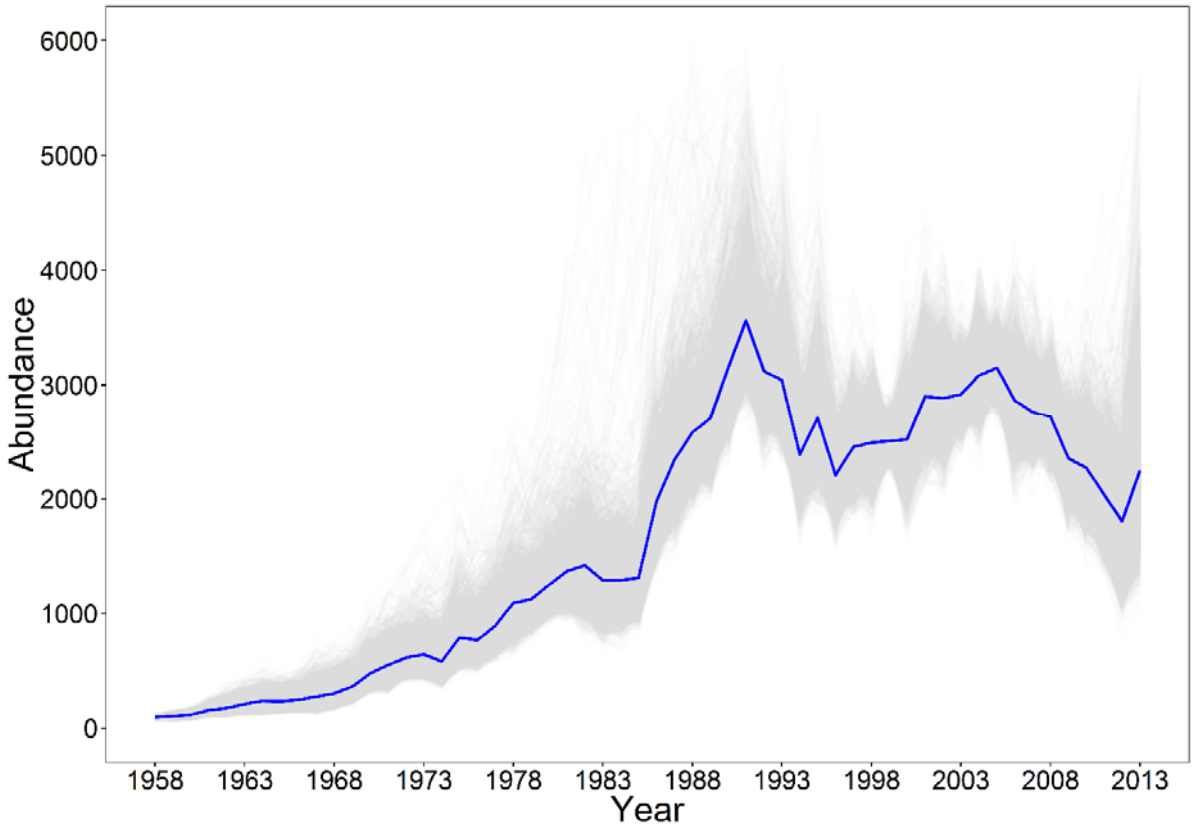

Fig. 3.2. Time series of statewide estimated moose abundances in Utah, 1958-2013. Gray lines indicate each model simulation after convergence, and the solid blue line indicates the median of all simulations.

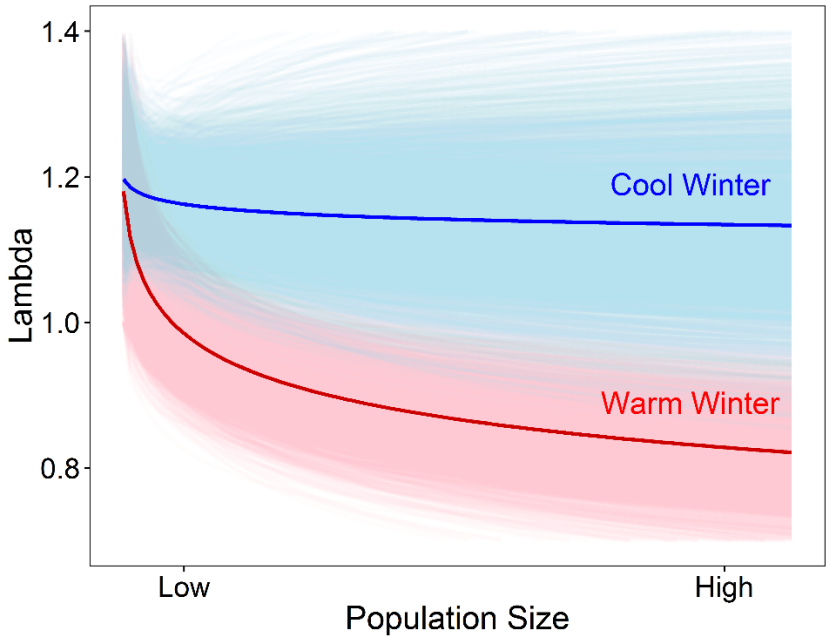

Fig. 3.3. The effect of the interaction between winter maximum temperature and population size on growth rate (lambda) for moose in northern Utah, USA under scenarios of cool (blue line, top) and warm (red line, bottom) winters. Each thin line represents a single model simulation and the thick lines represent the median of all simulations. At a low population size, winter maximum temperature has little effect on lambda. However, as population size increases, the magnitude of the effect of winter maximum temperature becomes greater.

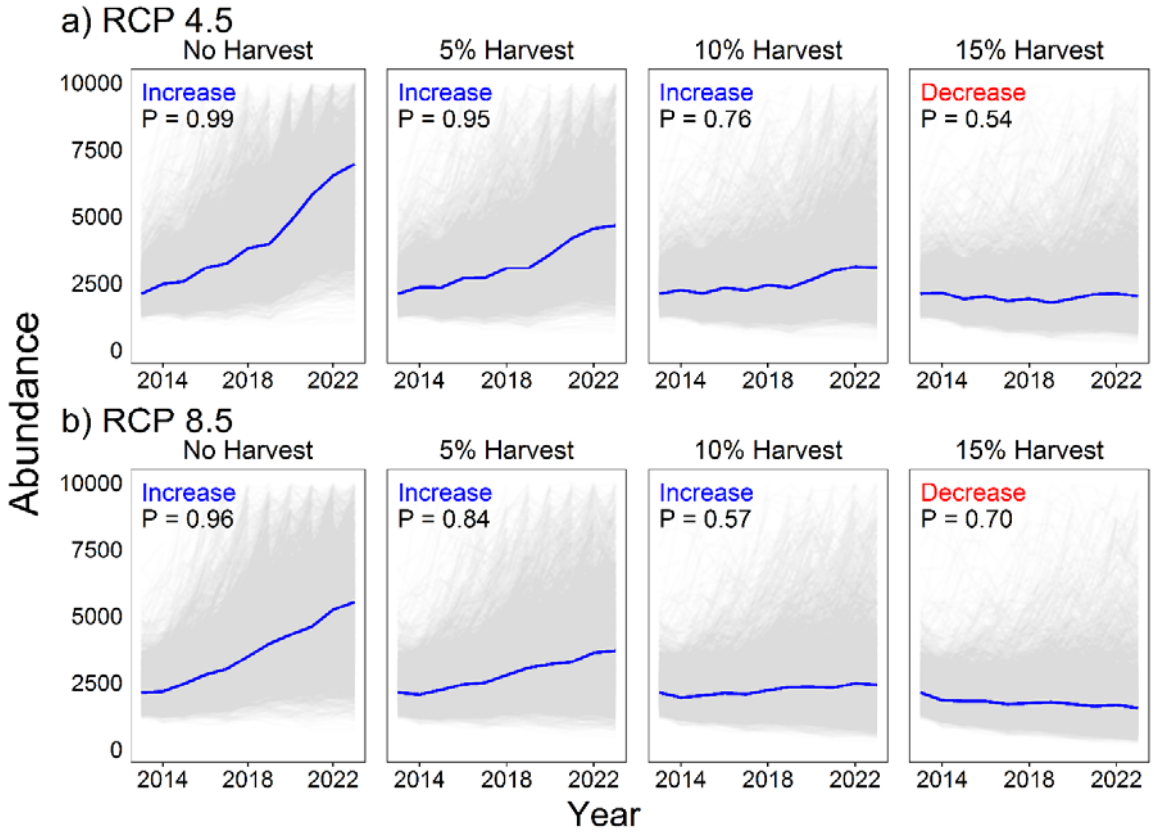

Fig. 3.4. Forecasted abundance estimates of moose in Utah between 2014-2023 under various scenarios of harvest rate and under two climate projection scenarios: a) Representative Concentration Pathway (RCP) 4.5 and b) RCP 8.5. Each scenario included 3 principal components as predictors which were constructed from the top-ranking climate variables from univariate climate models. The blue line indicates the median of all model simulations, and the gray lines represent each model simulation after convergence. P values indicate the probability of the trend observed (i.e. increase or decrease).

CHAPTER 4

CONCLUSION

This thesis contributes to a better understanding of the demography of moose in Utah, and more generally, the factors limiting populations of a cold-adapted species at its southern range limit. Although moose have been studied in detail across much of their distribution, our study focused on an understudied subspecies, the Shiras moose. Chapter 2 explored relationships between maternal age, body condition and reproductive output in moose in our study area. Chapter 3 examined the factors affecting population growth rates of moose in Utah and includes short term forecasts of moose abundance within the state. It is hoped that these results will aid in the management and conservation of moose to ensure their persistence within Utah.

The results of this work have both applied and theoretical value. Managers will benefit from a more thorough understanding of the factors limiting moose in their jurisdiction. Additionally, ecologists may find relevance to discussions involving how geographical gradients, or the location of a population within its species range, can lead to differences in vital rates and the factors that affect them.

Many of the results in this thesis are in direct accordance with a strong foundation of knowledge and theory of the demography of large herbivores. Other results suggest slight nuances in previously described patterns, which may owe to the unique geographic setting of this study population within the distribution of the species.

Chapter 1 supports earlier studies showing that maternal age and body condition are important factors in determining the reproductive success of ungulates. This finding

directly accords with patterns in which large herbivores living in seasonal environments rely on energy stores accumulated during periods of abundant primary productivity to utilize for reproductive costs in seasons when forage is more scarce. Additionally, we found evidence supporting patterns of reproductive senescence, particularly for pregnancy rates among moose older than 9 years. Both these patterns, though limited by sample size, suggest slight subtleties from earlier studies. First, the patterns we described relating subcutaneous fat reserves to pregnancy suggest that only a low threshold of fat was required for pregnancy, and the relationship was best described by a nonlinear model. This detail, although minor, has not been articulated for moose until this study. Second, our finding that pregnancy rates began to decline after age 9 suggests that reproductive senescence may occur earlier in our study system than those documented in previous studies. Finally, we provided evidence supporting an earlier hypothesis that moose reproductive rates tend to be lower in populations near the southern range limit, although determining the mechanism for this pattern will require further attention. These minor subtleties all contribute toward a more refined understanding of how moose in Utah differ from populations elsewhere.

Chapter 3 also provided results consistent with studies of large herbivores elsewhere, while highlighting differences specific to this system. First, we found direct evidence of density-dependence which acted to slow population growth in years of high population density. Although this is consistent with the theory of density-dependent resource limitation, detecting this effect can be difficult in natural systems which makes this a noteworthy finding. The negative effects of warm winter temperatures on

population growth of moose are in accordance with other studies at their southern range limit, but differ from the findings of studies conducted in the core of moose range. In addition to previous studies, we were able to provide evidence that the negative effect of winter temperature was operating through a density-dependent mechanism. Although we propose two explanations for this effect—relating to either winter tick abundance or a bottom-up effect of forage availability—the exact mechanism awaits further research. Nonetheless, this finding coincides with hypotheses regarding climatic limitation in southern moose populations, and generally accords with global patterns in which increases in temperature are affecting diverse groups of organisms.

Another benefit of this work was the application of time series models that are able to utilize imperfect datasets of population counts. Management agencies frequently collect abundance indices for populations of interest, but such datasets are often deemed unsuitable for rigorous analysis because of their imprecision. Additionally, when logistical constraints prevent data from being collected regularly, missing values make estimation of annual growth rates difficult. Further, a common problem results when managers seek to combine data across different sites (e.g. management units), but misalignment of the available data prevents counts from being summed across sites. We encountered each of these issues in our dataset, but the application of state-space models made an analysis of these data possible. We encourage others to adopt this approach to make inference from long-term datasets possible even when such datasets are imperfect. In particular, management agencies could benefit from such an approach to maximize inference on population processes from data with limited precision.

In conclusion, this thesis advances our understanding of the demography of an understudied population segment of moose. While this work is not an exhaustive assessment of the population dynamics of moose in Utah, it provides valuable baseline data and identifies areas where future research would be most beneficial.

APPENDICES

APPENDIX A

CHAPTER 1 SUPPLEMENTARY MATERIALS

Table A.1: Summary of adult female moose survival rates, Utah 2013–2015. Survival rates were calculated using a Kaplan-Meier survival estimator, i.e. $\hat{S}(t) = \prod \frac{n_i - d_i}{n_i}$ where n_i is the number of moose at risk at each interval, and d_i is the number of deaths occurring during each interval.

Year	***Study Area***	***Adult Survival Rate***	***95% CI***
2013	North Slope	87.1%	78.6–96.5%
	Wasatch	89.2%	81.4–97.8%
	Total	88.0%	82.1–94.4%
2014	North Slope	91.0%	81.6–100%
	Wasatch	85.7%	74.8–98.1%
	Total	88.0%	80.4–96.2%
2015	North Slope	91.5%	80.8–100%
	Wasatch	92.6%	83.2–100%
	Total	90.0%	77.7–100%

APPENDIX B

CHAPTER 2 SUPPLEMENTARY MATERIALS

APPENDIX B.1.—Model selection results for candidate models predicting the probability of pregnancy in adult moose in Utah, 2013. Models are presented in order of their AIC_c values. Knots refer to the placement (in mm) of breakpoints (linear splines) in scaled rump fat depth, and agecat refers to the age group of each moose, i.e. young, prime, or old.

Model Set	K	Log-likelihood	AICc	ΔAICc	Weight
Rump fat, knot = 2, agecat	5	-14.37	40.11	0.00	0.24
Rump fat, knot = 3, agecat	5	-14.47	40.30	0.19	0.22
Rump fat, knot = 4, agecat	5	-14.92	41.20	1.10	0.14
Rump fat, knot = 5, agecat	5	-15.36	42.07	1.97	0.09
Rump fat, knot = 1, agecat	5	-15.36	42.09	1.98	0.09
Rump fat, knot = 6, agecat	5	-15.80	42.97	2.87	0.06
Rump fat, knot = 7, agecat	5	-16.36	44.08	3.98	0.03
Rump fat, agecat	4	-17.72	44.33	4.23	0.03
Rump fat, knot = 3	3	-19.01	44.54	4.43	0.03
Rump fat, knot = 2	3	-19.06	44.65	4.54	0.02
Rump fat, knot = 4	3	-19.36	45.24	5.13	0.02
Rump fat, knot = 8, agecat	5	-16.96	45.28	5.17	0.02
Rump fat, knot = 5	3	-19.88	46.28	6.18	0.01
Rump fat, knot = 1	3	-20.08	46.68	6.58	0.01

Rump fat, knot = 6	3	-20.53	47.59	7.48	0.01
Rump fat, knot = 7	3	-21.29	49.10	9.00	0.00
Rump fat, knot = 8	3	-22.07	50.66	10.55	0.00
Rump fat	2	-23.35	50.96	10.86	0.00
intercept-only	1	-29.65	61.38	21.27	0.00

APPENDIX B.2.—Model selection results for candidate models predicting the probability of parturition among pregnant adult moose in Utah, 2013. Models are presented in order of their AIC_c values. Knots refer to the placement (in mm) of breakpoints (linear splines) in scaled rump fat depth, and agecat refers to the age group of each moose, i.e. young, prime, or old.

Model Set	K	Log-likelihood	AICc	ΔAICc	Weight
Rump fat	2	-15.02	34.51	0.00	0.13
Rump fat, knot = 4	3	-13.97	34.90	0.40	0.11
Rump fat, knot = 6	3	-14.03	35.02	0.52	0.10
Rump fat, knot = 3	3	-14.13	35.22	0.72	0.09
Rump fat, knot = 4, agecat	4	-12.87	35.40	0.89	0.08
Rump fat, knot = 5	3	-14.32	35.60	1.09	0.08
Rump fat, knot = 3, agecat	4	-13.02	35.71	1.20	0.07
Rump fat, agecat	3	-14.52	36.01	1.50	0.06
intercept-only	1	-17.08	36.31	1.80	0.05
Rump fat, knot = 6, agecat	4	-13.39	36.45	1.94	0.05
Rump fat, knot = 2	3	-14.76	36.47	1.97	0.05
Rump fat, knot = 5, agecat	4	-13.51	36.68	2.18	0.04
Rump fat, knot = 1	3	-14.96	36.87	2.37	0.04
Rump fat, knot = 2, agecat	4	-13.95	37.57	3.06	0.03
Rump fat, knot = 1, agecat	4	-14.30	38.26	3.75	0.02

APPENDIX B.3.—Model selection results for candidate models predicting the probability of recruiting a calf until March for pregnant adult moose in Utah, 2013. Models are presented in order of their AIC_c values. Knots refer to the placement (in mm) of breakpoints (linear splines) in scaled rump fat depth, and agecat refers to the age group of each moose, i.e. young, prime, or old.

Model Set	K	Log likelihood	AICc	ΔAICc	Weight
Rump fat	2	-11.63	27.93	0.00	0.22
Rump fat, knot = 4	3	-10.86	29.12	1.19	0.12
Rump fat, knot = 6	3	-10.92	29.25	1.32	0.11
Rump fat, knot = 5	3	-11.04	29.48	1.55	0.10
Rump fat, knot = 3	3	-11.22	29.85	1.91	0.08
Rump fat, agecat	3	-11.53	30.48	2.55	0.06
Rump fat, knot = 2	3	-11.61	30.64	2.70	0.06
Rump fat, knot = 1	3	-11.61	30.64	2.70	0.06
intercept-only	1	-14.34	30.89	2.96	0.05
Rump fat, knot = 4, agecat	4	-10.53	31.57	3.63	0.04
Rump fat, knot = 6, agecat	4	-10.78	32.06	4.12	0.03
Rump fat, knot = 5, agecat	4	-10.82	32.15	4.21	0.03
Rump fat, knot = 3, agecat	4	-10.95	32.40	4.47	0.02
Rump fat, knot = 1, agecat	4	-11.48	33.45	5.52	0.01
Rump fat, knot = 2, agecat	4	-11.48	33.45	5.52	0.01

APPENDIX B.4.—Results of a literature review on adult moose pregnancy rates in North America.

Study	Year	Location	Subspp.	Latitude	Annual Preg. Rate	N	Method	Overall Preg. Rate
this study	2013	NE Utah	*shirasi*	40.5	74	58	PSPB	74
K. L. Monteith and M. J. Kauffman, pers. comm.	2011	W. Wyoming	*shirasi*	42.8	53	19	PSPB	69
	2012		*shirasi*	42.8	66	47	PSPB	
	2013		*shirasi*	42.8	76	63	PSPB	
	2014		*shirasi*	42.8	68	40	PSPB	
Berger et al. 1999	1996	NW Wyoming	*shirasi*	43.8	84	25	FP	84
Houston 1968	1963–66	NW Wyoming	*shirasi*	43.8	95	19	FC	90
	1963–66	NW Wyoming	*shirasi*	43.8	86	22	RP	
Becker 2008	2004	NW Wyoming	*shirasi*	44	91	21	PSPB	92

	2005		*shirasi*	44	95	19	PSPB	
	2006		*shirasi*	44	90	19	PSPB	
Musante et al. 2010	2002	New Hampshire	*americana*	44.5	78	23	PSPB	78
N. J. DeCesare, pers. comm.	2013	W. MT	*shirasi*	45.45	64	11	PSPB	76
	2014		*shirasi*	45.45	88	16	PSPB	
	2015		*shirasi*	45.45	67	6	PSPB	
Boer 1987	1981–85	SE New Brunswick	*americana*	45.8	79	33	FC	79
Dodge et al. 2004	1999	N. Michigan	*americana*	46.7	78	18	PSPB	74
	2000		*americana*	46.7	70	27	FP	
	2001		*americana*	46.7	76	41	FP	
Severud et al. 2015	2013	NE Minnesota	*andersoni*	47.4	75	77	PR	75
N. J. DeCesare, pers. comm.	2013	N. Montana	*shirasi*	47.85	91	11	PSPB	76
	2014		*shirasi*	47.85	43	7	PSPB	

	2015		*shirasi*	47.85	100	3	PSPB	
Pimlott 1959	1951–56	S. Newfoundland	*americana*	48.1	77	132	FC	77
N. J. DeCesare, pers. comm.	2013	NW Montana	*shirasi*	48.17	83	12	PSPB	81
	2014		*shirasi*	48.17	100	7	PSPB	
	2015		*shirasi*	48.17	69	13	PSPB	
Bergerud et al. 1983, Bergerud and Snider 1988	1975–79	C. Ontario	*americana*	48.3	97	37	FC	97
Pimlott 1959	1951–56	E. Newfoundland	*americana*	48.5	87	38	FC	87
Pimlott 1959	1951–56	W. Newfoundland	*americana*	48.6	84	62	FC	84
Pimlott 1959	1951–56	C. Newfoundland	*americana*	48.9	77	132	FC	77
Crichton 1992	1986–91	Manitoba	*andersoni*	50	88	136	FC	88
Simkin 1965	1957–61	C. Ontario	*americana*	50.7	87	87	FC	87

Crichton 1988	1978–80	Hecla Island, Manitoba	*andersoni*	51.1	84	37	FC	84
Poole et al. 2007	2001–02	SE British Columbia	*andersoni*	50	80	39	PR	79
Thomson 1991	1986	Thomson Nikola, British Columbia	*andersoni*	50.9	80	54	FC	83
	1987		*andersoni*	50.9	83	86	FC	
	1988		*andersoni*	50.9	77	60	FC	
	1989		*andersoni*	50.9	93	96	FC	
	1990		*andersoni*	50.9	79	65	FC	
Thomson 1991	1985	Cariboo, British Columbia	*andersoni*	52.4	77	69	FC	80
	1986		*andersoni*	52.4	83	70	FC	
Heard et al. 1997	1977–95	C. British Columbia	*andersoni*	53.9	84	1025	FC	84

		Omineca, British						
Thomson 1991	1985	Columbia	*andersoni*	55.8	76	53	FC	81
	1986		*andersoni*	55.8	80	103	FC	
	1987		*andersoni*	55.8	90	83	FC	
	1988		*andersoni*	55.8	80	86	FC	
	1989		*andersoni*	55.8	80	86	FC	
	1990		*andersoni*	55.8	76	80	FC	
		Peace, British						
Thomson 1991	1988	Columbia	*andersoni*	56.9	83	193	FC	81
	1989		*andersoni*	56.9	80	159	FC	
	1990		*andersoni*	56.9	81	79	FC	
Lowe and Aderman 2014	1998	SW Alaska	*gigas*	59.5	100	25	PSPB	95
	2006		*gigas*	59.5	85	13	PSPB	
Oehlers et al. 2011	2003–05	Yakutat, Alaska	*gigas*	59.5	100	11	PSPB	100

Schwartz and Hundertmark 1993	1987–92	Kenai, Alaska	*gigas*	60.4	90	92	FC	90
Larsen 1989	1983–85	SW Yukon	*gigas*	60.7	84	43	RP	84
Welch et al. 2015	2009	SC Alaska	*gigas*	61.25	85	13	PSPB	93
	2010		*gigas*	61.25	94	18	PSPB	
	2011		*gigas*	61.25	100	14	PSPB	
Modafferi 1992	1964–74	SC Alaska	*gigas*	61.2	93	751	FC	93
Testa 2004, Testa and Adams 1998	1994	Nelchina, Alaska	*gigas*	62.4	86	7	FC	90
	1995		*gigas*	62.4	90	41	FC	
Ballard et al. 1991	1977	Nelchina, Alaska	*gigas*	62.6	88	59	RP	81
	1980		*gigas*	62.6	73	37	RP	
	1981		*gigas*	62.6	79	14	RP	
	1984		*gigas*	62.6	82	11	RP	
	1985		*gigas*	62.6	72	19	RP	

Gasaway et al. 1983	1975	Tanana Flats, Alaska	*gigas*	64	84	55	RP	84
Keech et al. 2000	1996	Tanana Flats, Alaska	*gigas*	64	98	44	PSPB	89
	1997		*gigas*	64	77	30	PSPB	
Gasaway et al. 1992	1984	E. Alaska	*gigas*	64	100	28	RP	100
Stenhouse et al. 1995	1986	Northwest Territories	*gigas*	64.9	96	27	RP	96
	1987		*gigas*	64.9	96	27	RP	
Bertram and Vivion 2002	1998	E. Interior Alaska	*gigas*	66.3	100	29	PSPB	100
	1999		*gigas*	66.3	100	26	PSPB	

APPENDIX B.5.—Results of a literature review on adult moose twinning rates in North America.

Study	Year	Location	Latitude	Annual Twinning Rate	N	Method	Overall Twinning Rate
this study	2013	NE Utah	40.5	5	42	DO	3
	2014		40.5	4	28	DO	
	2015		40.5	0	28	DO	
Becker 2008	2004	NW Wyoming	44	0	14	DO	7
	2005		44	11	19	DO	
	2006		44	8	12	DO	
Musante et al. 2010	2002	New Hampshire	44.5	21	14	DO	11
	2003		44.5	10	20	DO	
	2004		44.5	9	22	DO	
	2005		44.5	6	17	DO	
Murray et al. 2012	2006–09	Ontario	45	17	84	DO	17

Addison et al. 1985	1981		45.4	73	11	DO	44
	1982		45.4	78	9	DO	
	1983		45.4	45	11	DO	
	1984		45.4	17	24	DO	
N. J. DeCesare, pers. comm.	2013	W. Montana	45.45	0	7	DO	0
	2014		45.45	0	18	DO	
	2015		45.45	0	24	DO	
Boer 1987	1981–85	SE New Brunswick	45.8	26	31	IU	26
Aho and Hendrickson 1989	1985	N. Michigan	46.4	24	17	DO	37
	1986		46.4	43	7	DO	
	1987		46.4	25	24	DO	
	1988		46.4	69	16	DO	
	1989		46.4	33	12	DO	

Dodge et al. 2004	1999	N. Michigan	46.7	36	14	DO	20
	2000		46.7	6	18	DO	
	2001		46.7	21	24	DO	
Severud et al. 2015	2013	NE Minnesota	47.4	58	31	DO	58
N. J. DeCesare, pers. comm.	2013	N. Montana	47.85	0	5	DO	13
	2014		47.85	13	8	DO	
	2015		47.85	17	18	DO	
Albright and Keith 1987	1983–84	S. Newfoundland	47.9	1	107	DO	1
Pimlott 1959	1951–56	S. Newfoundland	48.1	5	99	IU	5
N. J. DeCesare, pers. comm.	2013	NW Montana	48.17	14	7	DO	4
	2014		48.17	0	11	DO	
	2015		48.17	0	10	DO	

Bergerud et al. 1983, Bergerud and Snider 1988	1975–79	C. Ontario	48.3	55	36	IU	56
Murray et al. 2006	1996–00	NW Minnesota	48.5	19	87	DO	20
Pimlott 1959	1951–56	E. Newfoundland	48.5	41	29	IU	41
Pimlott 1959	1951–56	W. Newfoundland	48.6	16	49	IU	16
Pimlott 1959	1951–56	C. Newfoundland	48.9	5	99	IU	5
Crichton 1992	1986–91	Manitoba	50	16	120	IU	16
Simkin 1965	1957–61	C. Ontario	50.7	29	76	IU	29
Crichton 1988	1978–80	Hecla Island, Manitoba	51.1	28	32	IU	28
Heard et al. 1997	1977–95	C. British Columbia	53.9	16	864	IU	16
Hauge and Keith 1981	1976	NE Alberta	57.1	22	9	DO	31
	1978		57.1	35	20	DO	

Lowe and Aderman							
2014	1998	SW Alaska	59.5	22	18	DO	60
	1999		59.5	92	13	DO	
	2000		59.5	59	27	DO	
	2001		59.5	55	20	DO	
	2002		59.5	94	18	DO	
	2003		59.5	67	21	DO	
	2004		59.5	53	30	DO	
	2005		59.5	70	30	DO	
	2006		59.5	71	21	DO	
	2007		59.5	54	24	DO	
	2008		59.5	52	21	DO	
	2009		59.5	34	29	DO	
	2010		59.5	71	28	DO	
	2011		59.5	64	22	DO	

Oehlers et al. 2011	2003–05	Yakutat, Alaska	59.5	63	11	DO	64
Franzmann and Schwartz 1985	1977	Kenai, Alaska	60.2	23	13	DO	54
	1978		60.2	22	36	DO	
	1982		60.2	67	52	DO	
	1983		60.2	72	50	DO	
Schwartz and Hundertmark 1993	1987–92	Kenai, Alaska	60.4	28	83	IU	28
MacCracken et al. 1997	1987	SC Alaska	60.5	0	16	DO	19
	1988		60.5	40	10	DO	
	1989		60.5	27	11	DO	
Larsen 1989	1983–85	SW Yukon	60.7	28	58	DO	28
Welch et al. 2015	2009	SC Alaska	61.25	0	5	DO	10
	2010		61.25	6	17	DO	
	2011		61.25	22	9	DO	

Modaferri 1992	1964–74	SC Alaska	61.2	21	695	IU	21
Boertje et al. 2007	2000–04	GMU 21E, Alaska	62.2	30	155	DO	30
Testa 2004, Testa and Adams 1998	1994	Nelchina, Alaska	62.4	9	77	DO	17
	1995		62.4	13	119	DO	
	1996		62.4	14	139	DO	
	1997		62.4	21	113	DO	
	1998		62.4	24	82	DO	
	1999		62.4	18	133	DO	
	2000		62.4	17	130	DO	
Ballard et al. 1991	1977	Nelchina, Alaska	62.6	23	71	DO	38
	1978		62.6	31	87	DO	
	1979		62.6	52	23	DO	
	1980		62.6	58	19	DO	
	1984		62.6	63	38	DO	

	1999; 2001–02;						
Boertje et al. 2007	2004	SC Alaska	62.6	24	338	DO	24
Keech et al. 2011	2001	W. Alaska	62.9	25	16	DO	41
	2002		62.9	46	68	DO	
	2003		62.9	31	64	DO	
	2004		62.9	35	62	DO	
	2005		62.9	47	85	DO	
	2006		62.9	38	89	DO	
	2007		62.9	51	86	DO	
Bowyer et al. 1998	1990–94	Denali, Alaska	63.5	48	46	DO	48
Boertje et al. 2007	2000–05	GMU 20D, Alaska	63.6	21	273	DO	21
Gasaway et al. 1983	1977–78	Tanana Flats, Alaska	64	32	35	DO	31

		Tanana Flats,					
Keech et al. 2000	1996	Alaska	64	31	35	DO	22
	1997		64	10	29	DO	
Boertje et al. 2007	1997–05	GMU 20A, Alaska	64	7	169	DO	7
Gasaway et al. 1992	1984	E. Alaska	64	52	27	DO	52
Boertje et al. 2007	2004–05	GMU 20E, Alaska	64	27	70	DO	27
Stenhouse et al. 1995	1986	NW Territories	64.9	30	10	DO	31
	1987		64.9	33	18	DO	
	1988		64.9	36	14	DO	
	1989		64.9	25	12	DO	
Boertje et al. 2007	1994–05	GMU 21D, Alaska	65.1	23	544	DO	23
Osborne et al. 1991	1988	Interior Alaska	65.1	48	42	DO	53
	1989		65.1	58	114	DO	
	1990		65.1	44	45	DO	
Boertje et al. 2007	1998–05	GMU 20B, Alaska	65.1	18	467	DO	18

Boertje et al. 2007	2003–05	GMU 24, Alaska	65.7	32	186	DO	32
Bertram and Vivion 2002	1998	E. Interior Alaska	66.3	66	27	DO	63
	1999		66.3	61	33	DO	
Boertje et al. 2007	1996–03	GMU 26A, Alaska	69.4	32	149	DO	32

APPENDIX B LITERATURE CITED

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APPENDIX C

CHAPTER 3 SUPPLEMENTARY MATERIALS

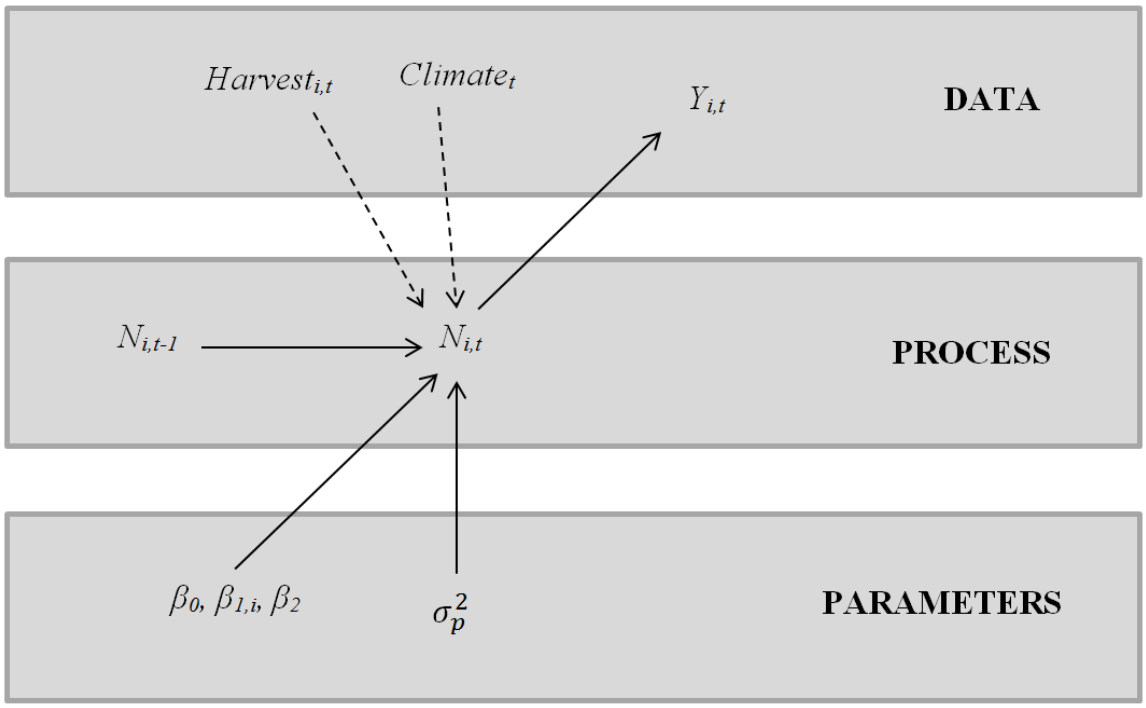

Fig. C.1. Directed acyclic diagram showing relationships between stochastic (solid lines) and deterministic (dotted lines) nodes for a state-space model describing population growth of moose in Utah, 1958–2013.